

Digestion Strategies of North Atlantic Seabirds

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This thesis is dedicated with love, to Robert Hilton and Phyllis Firth.

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ABSTRACT

Studies on digestion in North Atlantic seabirds are presented, with particular emphasis on the relationships between digestion and ecology. A negative relationship between the rate of digestion and digestive efficiency is shown to occur in an inter-specific comparison of eight North Atlantic seabird species. This relationship is interpreted as representing a trade-off between benefits of rapid digestion and benefits of high digestive efficiency. Digestion rate is related to gut morphology: species with small guts tend to have rapid digestion. The selection pressures which result in species adopting a given digestion strategy are considered. Species with opportunistic feeding habits, and which include low quality food in their diets, tend to have slow but efficient digestion, whereas species which specialise on highly digestible and energy dense fish prey tend to adopt a strategy of rapid but inefficient digestion. It is suggested that slow digestion and a large gut is a requirement for species consuming low quality prey. A modelling approach indicates that digestion strategy can also have a profound effect on time and energy budgets of seabirds. In terms of time and energy minimisation, rapid digestion is likely to be favoured when costs of flight to the foraging site are high (in energy or time). An ingestion bottleneck is identified, which limits feeding rates when the gut is full, and thus applies strong selection pressure on optimal feeding trip length.

The responses to digestive challenges of a specialist piscivore (Common Guillemot) and an opportunistically feeding seabird (Lesser Black-backed Gull) are compared. Birds were acclimated to one fish diet, and then abruptly switched to a novel diet. There is evidence that switched birds have non-optimal digestion of the novel diet, when compared with birds which are acclimated to that diet. The costs of diet switching are greater for Common Guillemots. The digestive cost of eating a mixed diet of two different fish types, when compared to eating the same diets separately, is also examined. For Common Guillemots digestive efficiency is significantly lower on the mixed diet, but no such cost is apparent for Lesser Black-backed Gulls. Thus the decision to change between diets should be affected by digestive considerations, even when the difference between diets is slight. It appears that species which commonly eat a varied diet are less affected by such digestive challenges.

The relationship between diet characteristics and retention time are examined in a range of seabird species. Different fish species are digested at different rates, and these differences tend to be consistent across seabird species. Ease of digestion, energy density and nutrient composition should be considered as separate attributes of a diet, all of which may affect optimal retention time. The criterion by which optimal retention time is set in seabirds is unclear: they may be net rate maximisers, or efficiency maximisers.

Geographic variation in the gut morphology and other major body organs is demonstrated within six Icelandic seabird species. This variation is consistent among species, and is related to geographic variation in ecological conditions, namely diet, foraging range and climate. Such variation in body composition between areas has not previously been shown, and may be an important component of adaptation to local habitat.

INTRODUCTION

Each chapter in this thesis has been submitted separately as a scientific paper, and therefore is a self-contained whole. The chapters are largely presented in the style of the journals to which they were submitted. In this general introduction I will briefly introduce some of the key ideas underlying the work, and summarise previous work on digestion in seabirds. I will then outline the structure of the thesis.

Theory of digestion strategies

This is a study of the links between digestion and ecology in seabirds. I examine how seabird species differ in their digestive function, and relate this to their feeding ecology and energetics. Studies of the interplay between digestion and ecology are not new. W.H. Karasov and co-workers have shown that digestion strategies and digestive constraints can have a profound effect on many ecological traits in birds, particularly diet choice (e.g. Karasov 1990; Martinez del Rio 1990; Martinez del Rio & Karasov 1990; Levey & Grajal 1991). Recently much work has also focused on how digestion can limit energy assimilation and ultimately energy expenditure in animals (Weiner 1992; Hammond & Diamond 1997).

The use of the comparative method and the behavioural ecology concepts of trade-offs and optimality to explain differences in digestion parameters between species has underpinned the advances made in recent years. Sibly (1981) gave a common framework to various studies of digestion by suggesting the idea of an energy gain curve that describes the net energy gain from a meal with time after ingestion. He used this to show that, under various optimisation criteria, there is an optimal digesta retention time, which could be predicted if the shape of the energy gain curve were known. This explicitly linked retention time to digestive efficiency: for an individual eating any particular meal, the proportion of the total energy content which is extracted is a function of the time that the digesta is held in the gut. Differences between diets in their ease of breakdown, or in the total amount of energy which they contain, will cause variations in the shape of the energy gain curve. Differences between consumers in the rate at which they can break down and assimilate diets will cause between-consumer variation in energy gain curves when eating the same diet. In general reviewers have suggested that diet-based variation in

digestion parameters is of greater magnitude than consumer-based variation (Warner 1981; Castro, Stoyan & Myers 1989; Karasov 1990). Another important point, to which Sibly (1981) briefly alluded, is that factors other than digestion might have an influence on optimal retention times. He suggested that birds benefit from being light because of the high and mass-dependent energy cost of flight. Since excretion is a mass-reducing activity, short digesta retention times might bring energetic advantages. This hints at the need for optimal retention times to be seen as affected not just by the diet consumed but by other ecological factors. For instance the benefits of minimising mass might vary between individuals within a species, or between species within a feeding guild. This issue is explored in Chapter 3, in which I model the optimal retention time of two contrasting seabird species. I attempt to use a more inclusive measure of the fitness of a given digestion strategy, by incorporating the overall effects of retention time and digestive efficiency on time and energy budgets.

Sibly's ideas were expressed mathematically by Karasov (1996) who described it as the digestive adaptation paradigm:

$$\text{digestive efficiency} \propto \frac{(\text{retention time} \cdot \text{reaction rate})}{(\text{energy density} \cdot \text{digesta volume})}$$

where energy density is the energy content per unit mass of digesta, and reaction rate comprises hydrolysis and absorption rates.

In general, work on relationships between ecology and digestion has been conducted on plant-eating animals, whether frugivorous, herbivorous, granivorous or nectarivorous (see Karasov 1990; 1996). This bias mainly stems from the observation that plant matter tends to pose more problems for consumers than does animal matter. Plant matter can be refractory to digestion, contain unbalanced nutrients or toxic chemicals, and be very energy dilute. Thus one would expect that assimilation of sufficient nutrient from the diet would be a major problem for plant-eaters. By contrast, vertebrate tissues are rather easy to digest, and have similar nutrient composition to vertebrate consumers, so one might expect that digestion-related constraints on meat-eaters would be rare (Stevens & Hume 1995).

Digestion in seabirds

Digestion in seabirds has been little studied. Most interest has centred on the peculiar digestion of Procellariiformes. Many of these species have unusual catalytic enzymes (chitinases and wax esterases) in order to break down their prey of marine planktonic invertebrates (Obst 1986; Place & Roby 1986; Roby, Place & Ricklefs 1986; Jackson, Place & Seiderer 1992; Place 1992). They also have a mechanism for concentrating the lipid component of their diet in a large distensible stomach, while allowing the aqueous component to pass more quickly through the digestive tract (Duke, Place & Jones 1989; Roby, Brink & Place 1989). This results in very long digesta retention times, particularly of the lipid phase, with consequently high digestive efficiencies (Roby, Brink & Place 1989; Jackson & Place 1990). Table 1 shows published digestive efficiencies of seabird species, or other piscivores. Measures of digesta retention time in seabirds are much scarcer in the literature. Jackson (1992) gives detailed figures for five Southern Hemisphere seabird species, and data for Jackass Penguins (*Spheniscus demersus*) and Cape Gannets (*Morus capensis*) are reported by Duffy *et al.* (1985) and Laugskch & Duffy (1986). Thus this study provides novel basic information on digestion parameters of seabirds; in particular it gives data on digestion in North Atlantic seabird species, redressing the bias in the literature towards the Southern Ocean Procellariiformes and Sphenisciformes. North Atlantic seabird communities are dominated by Charadriiformes (gulls, auks and skuas) (Furness & Monaghan 1987), and digestion in these taxa has been very little studied (but see Brekke & Gabrielsen 1994).

Although published studies on digestion in fish eating birds and seabirds have been few, and rather *ad-hoc*, a major exception is the work of Sue Jackson (1990). She discussed many of the issues with which I am concerned in this study, notably the effect of mass constraints on digestion strategies, links between digestion and metabolic rates, and the relative costs and benefits of digestive specialisation and opportunism.

Digestion strategies of birds of prey

I aim to develop ideas suggested by Nigel Barton (1992) in his thesis on digestion strategies in raptors. He demonstrated a link between retention time of digesta, the efficiency of digestion, and gross gut morphology; he then showed an association between these traits and the feeding methods employed by raptor species. Raptor species with long digesta retention times tend to have higher digestive efficiency than those with short retention times. Furthermore variations in the length of the small intestine seem to explain the variations in digesta retention time. Species with long small intestines have longer digesta retention times than species with short small intestines. In **Chapter 1** we show that digesta flow rate, crudely calculated as the length of the small intestine divided by the retention time of digesta, increases as small intestine length increases. There is almost no scatter about the calculated regression, which implies that deviations from the predicted flow rate do not explain retention time variations. However, the exponent of the regression is such that flow rate increases do not fully compensate for intestine length increases, and hence species with long small intestines tend to have long digesta retention times. Finally Barton (1992) showed that digestion parameters in raptor species are associated with feeding ecology. Species which actively pursue fast moving, live, mainly avian prey (“pursuers”) tend to have short retention times and short small intestines, and consequently to have low digestive efficiency. Species which eat mainly carrion and/or which drop onto slow moving prey from above (“searchers”), have long retention times, high digestive efficiency, and long small intestines. Barton suggested that pursuit predators adopt a short retention time strategy because mass minimisation is crucial to their hunting success. Acceleration, turning speed and maximum speed in flight are all strongly mass-dependent (Andersson & Norberg 1981), and pursuit raptors typically have very low attack success rates (Temeles 1985), so reducing mass through rapid excretion is likely to be a good strategy, even though the cost is a somewhat lower digestive efficiency. By contrast, searching predators do not rely on flying ability to capture prey, and therefore their success rates are unlikely to be mass dependent. They thus adopt a strategy of long digesta retention times, which gives the benefit of high digestive efficiency. It was suggested that the rapid but inefficient digestion of pursuit predators acts as a

constraint on their diet choice. Pursuit predators are unable to use low quality diets, such as carrion, because they cannot process quantities sufficient to maintain body mass at their low digestive efficiency. It was suggested that this explained why many pursuit foraging raptors apparently ignore readily available carrion as a potential food item.

Outline of the thesis

The main focus of this study falls on two critical digestion parameters - retention time and digestive efficiency. These two parameters have important knock-on effects on animal energetics, and are causally linked in a negative relationship; together they constitute an animal's "digestion strategy" (Milton 1981; Sibly 1981). The emphasis is on differences in digestion strategy between species within the same feeding guild. Guild members use different feeding methods to exploit the food resource; here I examine how different digestion strategies are used in association with these feeding methods.

I aim firstly to measure retention time and digestive efficiency of a number of seabird species, and test for an inter-specific trade-off between the two parameters (**Chapter 2**). I also examine whether digestion strategy is related to feeding ecology as it is for raptor species. The pursuer - searcher dichotomy is problematic for seabirds, because pursuit in piscivores is generally conducted underwater. The effects of mass on underwater pursuit ability are unknown, and indeed it is not even known whether catching a fish is typically a demanding job (R. Wilson *pers comm.*). It may be that for most seabirds, locating dense shoals of fish is the limiting factor, and that once found, catching the fish in the shoal is rather easy. However, recalling that the pursuer - searcher dichotomy is also associated with dietary differences, I relate digestion strategies in seabird species to their typical diets. Species are divided into two categories: "generalists", which eat a wide variety of food types, including invertebrates and vegetable matter, which can be resistant to digestion, and lower in energy density than fish; and "specialists" which eat mainly fish which are relatively easy to digest and high in energy content.

For raptors there was a clear explanation for the observed between-species variation in digestion strategy - that of the benefits of mass-minimisation, which are greater

for pursuit predators than for searchers. However, whether this intuitive explanation is valid depends on the details of birds' time and energy budgets. If pursuers' meals are infrequent, then rapid excretion may not be necessary to bring them to a low mass before the next hunt. If searchers spend a large proportion of each day in flight then they may make large energetic savings by rapidly excreting digesta. Furthermore, for seabirds the distinction is problematic anyway, because pursuit foraging underwater is poorly understood. Therefore I conducted a modelling exercise (**chapter 3**) in order to clarify the ecological factors which might affect optimal digestion strategies. A contrast is drawn between two seabird species which differ in their feeding ecology - the Herring Gull and the Common Guillemot. Realistic time-energy budgets are developed for both species, and the effect of varying digestion strategy on the daily foraging time and energy expenditure is examined

Having established that digestion strategies do vary between seabird species, in a manner consistent with the idea of a retention time – digestive efficiency trade-off, I move on to examine the digestion strategies of seabird species in more detail (**chapter 4**). I aim to test some hypotheses concerning the cost to digestive function of switching and mixing diets, and how these costs might differ between “generalist” feeders and “specialist” feeders. It has been shown that digestive function in animals shows large-scale reversible plasticity, in response to changes in the nature and quantity of the diet. This issue is discussed at length by Karasov (1996). If an animal “fine-tunes” its digestion in order to meet the demands of its current diet, then it will initially have sub-optimal digestive function if forced to switch to a different diet. Likewise an animal cannot optimise digestive function on more than one diet simultaneously, and thus when eating a mixed diet it should show reduced digestive performance compared to its performance on the component diets when eaten separately. The idea of an initial cost of switching has already been examined in species which switch between fruit, seeds, and insect diets (Levey & Karasov 1989; Lodge 1994; Afik & Karasov 1995). These represent gross shifts in the characteristics of the diets. Such shifts do occur seasonally in the diet of many temperate passerine species. However, I wished to determine whether there is also a cost associated with switches between subtly different diets, in this case between two

small shoaling marine fish, which differ in their lipid content. Such small-scale changes in diet must be very frequent in nature. In seabirds, abrupt switches in diet between one fish species and another are common during the breeding season, presumably in response to changes in shoal availability (Furness & Monaghan 1987). The issue of diet mixing, and its potential to reduce digestive performance has not been addressed before. I also compare the relative ability of Lesser Black-backed Gulls and Common Guillemots to deal with the “digestive challenges” of switching and mixing diets. The former species is a generalist, which eats a varied diet, including invertebrates and vegetable matter, whereas the latter is a specialist piscivore (Cramp & Simmons 1983; Cramp 1985). I test the prediction that gulls will suffer lower costs when confronted with digestive challenges than Common Guillemots.

In the multi-species comparison described in chapter 2, two different experimental diets were used: Lesser Sandeel and Whiting. Retention time of the latter was consistently longer than retention time of the former. I therefore use Sibly’s (1981) idea of an optimal retention time to investigate further how characteristics of the diet affect retention times (**chapter 5**). I describe three different characteristics of the diets: chemical composition, energy content, and the ease of breakdown in the digestive tract (using an *in vitro* assay developed by Jackson, Duffy & Jenkins (1987)). The predicted ranking of optimal retention times is compared with the observed ranking when the fish species are fed to seabirds. One of the key points raised is that the different characteristics of the diets act separately to influence optimal retention times, although this has tended to be overlooked in previous studies.

In **chapter 6** I present data on how the morphology of the gut, and other major body organs shows adaptive variation within species. For six seabird species sampled during the breeding season in Iceland I analyse intraspecific organ mass variation between two areas which differ in ecological conditions. The morphology of the gut is related to characteristics of the diets which were elucidated in chapter 5. Variation in heart, liver, kidney and flight muscle mass in relation to foraging range and climate are also considered.

Table 1: Previous measures of digestive efficiency in piscivorous birds

species	diet	efficiency measure ¹	efficiency ²	n ³	origin of birds	reference
King Penguin <i>Aptenodytes patagonicus</i>	Squid	AMEC	81.3	4	wild adults	Adams 1984
	Pilchard	TMEC	70.89±9.99	6	wild adults	Jackson 1990
	Squid	TMEC	79.88±1.87	5		
	Prawn	TMEC	72.89	2		
Emperor Penguin <i>Aptenodytes forsteri</i>	Arrow Squid	AMEC	76.2±1.2	3	wild adults	Robertson & Newgrain 1992
	Australian Salmon	AMEC	81.8±0.9	2		
	Antarctic Krill	AMEC	70.5±1.7	3	wild adults	Kirkwood & Robertson 1997
	Sandy Sprat	AMEC	70.5±0.8	3	wild adults	
Little Penguin <i>Eudyptula minor</i>	Gould's Squid (mantles)	AMEC	73.0±1.5	3		Gales 1989
	Squid	AMEC	51-77	3	captive reared	Heath & Randall 1985
Jackass Penguin <i>Spheniscus demersus</i>	Anchovy	AMEC	78-88	3	chicks	
	Mullet	AMEC	77-87	3		
	Anchovy	AMEC	75.3	4	captive reared chicks	Cooper 1977
Gentoo Penguin	Pilchard	TMEC	78.08±3.49	6	wild adults	Jackson 1990

species	diet	efficiency measure ¹	efficiency ²	n ³	origin of birds	reference
<i>Pygoscelis papua</i>	Squid Prawn	TMEC TMEC	76.44±4.61 78.20±4.76	6 3		
Rockhopper Penguin	Pilchard	TMEC	75.13±5.81	6	wild adults	Jackson 1990
<i>Eudyptes chrysocome</i>	Squid	TMEC	76.98±4.78	6		
	Prawn	TMEC	79.31±4.72	6		
Sooty Albatross	Pilchard	TMEC	76.51±1.59	5	wild adults	Jackson 1990
<i>Phoebastria fusca</i>	Squid	TMEC	75.62±1.31	5		
	Prawn	TMEC	78.43±2.87	5		
Blue Petrel	Pilchard	TMEC	77.42±2.17	6	wild adults	Jackson 1990
<i>Halobaena caerulea</i>	Squid	TMEC	68.32±2.30	6		
	Prawn	TMEC	74.54±7.18	6		
White-chinned Petrel	Light-fish	TMEC	75.61±2.03	5	wild fledglings	Jackson 1990
<i>Procellaria</i>	Squid	TMEC	76.58±1.93	5		
<i>aequinoctialis</i>	Antarctic Krill	TMEC	75.79±1.69	5		
White Pelican	fish	AMEC	73			Cooper 1980
<i>Pelecanus onocrotalis</i>						
Cape Gannet	Pilchard	AMEC	79.4	1	captive reared	Batchelor & Ross 1984
<i>Morus capensis</i>	Stockfish	AMEC	69.2	1	chicks	

species	diet	efficiency measure ¹	efficiency ²	n ³	origin of birds	reference
Cape Gannet <i>Morus capensis</i>	Anchovy	AMEC	76.1	2	captive reared chicks	Cooper 1978
	Anchovy	AMEC	74.5	2	wild juvenile	
	Pilchard	TMEC	75.53±1.48	5	wild adult	Jackson 1990
	Squid	TMEC	72.18±3.06	5		
	Prawn	TMEC	70.78±3.48	5		
Double-crested Cormorant	Channel Catfish	AMEC _N	79.7±1.36	4	wild adults in	Brugger 1993
	Gizzard Shad	AMEC _N	77.6±1.51	3	wildlife	
<i>Phalacrocorax auritus</i>	Bluegill	AMEC _N	74.7±3.02	4	rehabilitation centre	
	eviscerated Pollack	AMEC	84.9	9	wild chicks	Dunn 1975
Great Blue Heron <i>Ardea herodias</i>	Herring	TMEC _N	65.9±15.9	8	captive reared	Bennett & Hart 1993
	Mackerel	TMEC _N	86.6±3.8	8	adults	
	Trout	TMEC _N	87.0±2.1	8		
Wood Stork <i>Mycteria americana</i>	Fish	AMEC	79.0	?	captive reared adults	Kahl 1964
White Ibis <i>Eudocimus albus</i>	Shrimp & Anchovy	AMEC	79.7	?	captive reared chicks	Kushlan 1977
Black-headed Gull	Heart	AMEC	87.1	8	captive reared	Nelsen & Brandl 1988

species	diet	efficiency measure ¹	efficiency ²	n ³	origin of birds	reference
<i>Larus ridibundus</i>	Trout	AMEC	78.5	8	chicks	
	Whitebait	AMEC	76.6	8		
	Earthworms	AMEC	69.6	8		
Black-legged Kittiwake	Capelin	AMEC _N	77.5±1.4	10	wild adults	Brekke & Gabrielsen 1994
<i>Rissa tridactyla</i>	Arctic Cod	AMEC _N	83.1±0.7	8		
Brunnich's Guillemot	Capelin	AMEC _N	70.6±0.6	9	wild adults	Brekke & Gabrielsen 1994
<i>Uria lomvia</i>	Arctic Cod	AMEC _N	74.7± 0.9	5		

¹ AMEC = Apparent Metabolizable Energy Coefficient

TMEC = True Metabolizable Energy Coefficient

_N = correction made for Nitrogen retention.

² figures are means; standard deviations are given where available.

³ number of birds used in trial.

LITERATURE CITED

- Adams, N.J (1984) Utilization efficiency of a squid diet by adult King Penguins (*Aptenodytes patagonicus*). *Auk* **101**, 884-886.
- Afik, D. & Karasov, W.H. (1995) The trade-offs between digestion rate and efficiency in warblers and their ecological implications. *Ecology* **76**, 2247-2257.
- Andersson, M. & Norberg, R.A. (1981) Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biological Journal of the Linnean Society* **15**, 105-130.
- Barton, N.W.H. (1992) Morphological adaptation and digestion in relation to raptor feeding ecology. PhD thesis, University of Glasgow.
- Batchelor, A.L. & Ross, G.J.B. (1984) The diet and implications of dietary change of Cape Gannets on Bird Island, Algoa Bay. *Ostrich* **55**, 45-63.
- Bennett, D.C. & Hart, L.E. (1993) Metabolizable energy of fish when fed to captive Great Blue Herons (*Ardea herodias*). *Canadian Journal of Zoology* **71**, 1767-1771.
- Brekke, B. & Gabrielsen, G.W. (1994) Assimilation efficiency of adult Kittiwakes and Brünnich Guillemots fed Capelin and Arctic Cod. *Polar Biology* **14**, 279-284.
- Brugger, K.E. (1993) Digestibility of 3 fish species by Double-crested Cormorants. *Condor* **95**, 25-32.
- Castro, G., Stoyan, N. & Myers, J.P. (1989) Assimilation efficiency in birds: a function of taxon or food type? *Comparative Biochemistry and Physiology* **92A**, 271-278.
- Cooper, J. (1977) Energetic requirements for growth of the Jackass Penguin. *Zoologica Africana* **12**, 201-213.
- Cooper, J. (1978) Energetic requirements for growth and maintenance of the Cape Gannet (Aves; Sulidae). *Zoologica Africana* **13**, 305-317.
- Cooper, J. (1980) Energetic requirements for maintenance of a captive juvenile Great White Pelican *Pelecanus onocrotalus*. *Cormorant* **8**, 17-19.

- Cramp, S. (1985) *Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic; Volume 4: Terns to Woodpeckers*. Oxford University Press, Oxford.
- Cramp, S., & Simmons, K.E.L. (1983) *Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic; Volume 3: Waders to Gulls*. Oxford University Press, Oxford.
- Duffy, D.C., Furness, B.L., Laugsch, R.C. & Smith, J.A. (1985) Two methods of measuring food transit rates of seabirds. *Comparative Biochemistry & Physiology* **82A**, 781-785.
- Duke, G.E., Place, A.R. & Jones, B. (1989) Gastric emptying and gastrointestinal motility in Leach's Storm Petrel chicks (*Oceanodroma leucorhoa*). *Auk* **106**, 80-85.
- Dunn, E.H. (1975) Caloric intake of nestling Double-crested Cormorants. *Auk* **92**, 553-565.
- Furness, R.W. & Monaghan, P. (1987) *Seabird Ecology*. Blackie, Edinburgh.
- Gales, R. (1989) Validation of the use of tritiated-water, doubly labeled water, and Na-22 for estimating food, energy, and water-intake in Little Penguins, *Eudyptula minor*. *Physiological Zoology* **62**, 147-169.
- Hammond, K.A. & Diamond, J. (1997) Maximal sustained energy budgets in humans and animals. *Nature* **386**, 457-462.
- Heath, R.G.M. & Randall, R.M. (1985) Growth of Jackass Penguin chicks (*Spheniscus demersus*) hand reared on different diets. *Journal of Zoology* **205**, 91-105.
- Jackson, S. (1990) Seabird digestive physiology in relation to foraging ecology. PhD Thesis, University of Cape Town, Rondebosch, South Africa.
- Jackson, S. (1992) Do seabird gut sizes and mean retention times reflect adaptation to diet and foraging method? *Physiological Zoology* **65**, 674-697.
- Jackson, S., Duffy, D.C. & Jenkins, J.F.G. (1987) Gastric digestion in marine vertebrate predators: *in vitro* standards. *Functional Ecology* **1**, 287-291.

- Jackson, S. & Place, A.R. (1990) Gastrointestinal transit and lipid assimilation efficiencies in three species of sub-antarctic seabird. *Journal of Experimental Zoology* **255**, 141-154.
- Jackson, S., Place, A.R. & Seiderer, L.J. (1992) Chitin digestion and assimilation by seabirds. *Auk* **109**, 758-770.
- Kahl, M.P. (1964) Food ecology of the Wood Stork (*Mycteria americana*) in Florida. *Ecological Monographs* **34**, 97-117.
- Karasov, W.H. (1990) Digestion in birds: chemical and physiological determinants and ecological implications. *Studies in Avian Biology* **13**, 391-415.
- Karasov, W.H. (1996) Digestive plasticity in avian energetics and feeding ecology. *Avian Energetics* (ed C. Carey), pp. 61-84, Chapman & Hall, New York.
- Kirkwood, R. & Robertson, G. (1997) The energy assimilation efficiency of Emperor Penguins, *Aptenodytes forsteri*, fed a diet of Antarctic Krill, *Euphausia superba*. *Physiological Zoology* **70**, 27-32.
- Kushlan, J.A. (1977) Growth energetics of the White Ibis. *Condor* **79**, 31-36.
- Laugsch, R.C. & Duffy, D.C. (1986) Food transit rates in Cape Gannets *Morus capensis* and Jackass Penguins *Spheniscus demersus*. *Condor* **88**, 117-119.
- Levey, D.J. & Grajal, A. (1991) Evolutionary implications of fruit processing limitations in Cedar Waxwings. *American Naturalist* **138**, 171-189.
- Levey, D.J. & Karasov, W.H. (1989) Digestive responses of temperate birds switched to fruit or insect diets. *Auk* **106**, 675-686.
- Lodge AJ (1994) The effect of diet quality and environmental factors on gut structure and function in the Starling, *Sturnus vulgaris* (L.). PhD thesis, University of Reading.
- Martinez del Rio, C. (1990) Dietary, phylogenetic, and ecological correlates of intestinal sucrase and maltase activity in birds. *Physiological Zoology* **63**, 987-1011.
- Martinez del Rio, C. & Karasov, W.H. (1990) Digestion strategies in nectar-eating and fruit-eating birds and the sugar composition of plant rewards. *American Naturalist* **136**, 618-637.

- Milton, K. (1981) Food choice and digestive strategies of two sympatric primate species. *American Naturalist* **117**, 476-495.
- Nelsen, I. & Brandl, R. (1988) Utilization of different diets by hand-reared Black-headed Gull nestlings (*Larus ridibundus*). *Zool. Anz.* **220**, 291-299.
- Obst, B.S. (1986) Wax digestion in Wilson's Storm-Petrel. *Wilson Bulletin* **98**, 189-195.
- Place, A.R. (1992) Comparative aspects of lipid digestion and absorption - physiological correlates of wax ester digestion. *American Journal of Physiology* **263**, R 464-R 471.
- Place, A.R. & Roby, D.D. (1986) Assimilation and deposition of dietary fatty alcohols in Leach's Storm Petrel, *Oceanodroma leucorhoa*. *Journal of Experimental Zoology* **240**, 149-161.
- Robertson, G. & Newgrain, K. (1992) Efficacy of the tritiated-water and Na-22 turnover methods in estimating food and energy-intake by Emperor Penguins *Aptenodytes forsteri*. *Physiological Zoology* **65**, 933-951.
- Roby, D.D., Brink, K.L. & Place, A.R. (1989) Relative passage rates of lipid and aqueous digesta in the formation of stomach oils. *Auk* **106**, 303-313.
- Roby, D.D., Place, A.R. & Ricklefs, R.E. (1986) Assimilation and deposition of wax esters in planktivorous seabirds. *Journal of Experimental Zoology* **238**, 29-41.
- Sibly, R.M. (1981) Strategies of digestion and defaecation. *Physiological Ecology: an evolutionary approach to resource use* (eds C.R. Townsend & P. Calow), pp.109-139, Blackwell Scientific Publications, Oxford.
- Stevens, C.E., & Hume, I.D. (1995) *Comparative physiology of the vertebrate digestive system*. Cambridge University Press, Cambridge.
- Temeles, E.J. (1985) Sexual size dimorphism of bird-eating hawks: the effect of prey vulnerability. *American Naturalist* **125**, 485-499.
- Warner, A.C.I. (1981) Rate of passage of digesta through the gut of mammals and birds. *Nutrition Abstracts and Reviews Series B* **51**, 789-820.

Weiner, J. (1992) Physiological limits to sustainable energy budgets in birds and mammals - ecological implications. *Trends in Ecology & Evolution* **7**, 384-388.

chapter 1

ECOLOGICAL CONSTRAINTS ON DIGESTIVE PHYSIOLOGY IN CARNIVOROUS AND PISCIVOROUS BIRDS

In press as:

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Ecological constraints on digestive physiology in carnivorous and piscivorous birds.
Journal of Experimental Zoology.

Dr. Nigel Barton gathered the data presented in this chapter on digestion in raptors.
The analyses of these data were conducted in part by Dr. Barton (1992), and in part
by myself. I wrote the manuscript.

ABSTRACT

Digestion strategies of meat and fish eating birds have received little attention, and the assumption has generally been made that there is rather little variation in digestion parameters between species in these guilds. We show that there is significant though small variation between species in apparent absorption efficiency. This variation is associated with an apparent trade-off between retention time of digesta and apparent absorption efficiency: short retention times result in low apparent absorption efficiency. We show that, in raptors, rapid digestion is a consequence of both reduced gut length, and increased flow rate of digesta. We examine the ecological correlates of digestive strategy in raptors and seabirds. Rapid digestion appears to be associated with a pursuit foraging mode, whereas slow digestion tends to occur in species with a searching foraging mode. We suggest that in raptors which actively pursue aerial prey, the mass savings that can be achieved through rapid digestion exceed the costs in reduced apparent absorption efficiency. However, a species which adopts a strategy of rapid but inefficient digestion may be restricted in diet to high quality food types, whereas species with a slow but efficient digestive strategy are able to exploit a wider range of food types, including low quality prey.

INTRODUCTION

Plant eating birds and mammals show considerable variation in the structure and action of their digestive tracts (McLelland, '79; Duke, '86; McNeill Alexander, '93; Karasov and Hume, '96). The guts of many herbivores show specialisations that assist the digestion of plant matter, in particular by breaking down cellulose cell walls in order to assimilate cell contents. Examples of such specialisations in birds include the fermentation chambers found in the foregut of the folivorous Hoatzin (*Opisthocomus hoatzin*) (Grajal et al., '89), and in the hindgut of Tetraonidae (Leopold, '53); conversely some Anserinae extract sufficient energy and nutrient from a plant diet by processing large quantities very quickly with low efficiency, and minimal microbial fermentation (Sedinger et al., '89). As well as frequently being refractory to digestion (Van Soest, '82), plant matter is also diverse in nature. Herbivorous birds and mammal species may be folivorous, frugivorous, nectarivorous, granivorous, or florivorous; they may eat root tubers, or suck sap. The difficulty and diversity of plant digestion has prompted much research into the ecological causes and effects of different digestion strategies. Topics such as the restrictions on diet choice imposed by a given digestive strategy (e.g. Milton, '81; Van Soest, '82; Kehoe and Ankney, '85; Barnes and Thomas, '87; Levey and Karasov, '89; Levey and Karasov, '92), optimal retention times for different food types (e.g. Karasov and Levey, '90; Prop and Vulink, '92), temporal variation in digestive organ morphology (e.g. Ankney, '77, Pulliainen and Tunkkari, '83; Lee and Houston '93; Leif and Smith, '93; Lee and Houston '95) and energy expenditure bottlenecks (e.g. Kenward and Sibly, '77; Diamond et al., '86; Weiner, '92) have been studied in herbivores and seasonal herbivores.

By contrast, comparatively little attention has been given to the ecological implications of digestion in predatory birds and mammals (but see Place and Roby, '86; Place et al., '86; Jackson, '90). This is probably because vertebrate tissues are relatively simple to digest, and tend to be rather uniform in nature (Kirkwood, '85). Provided acidic conditions and suitable proteolytic enzymes are present in the stomach, animal protein can be speedily digested without the need for any complicated fermentation chambers. One might therefore imagine that all vertebrate predators would break down food in a similar way, and with similar efficiency. This

was indeed the conclusion of two literature reviews of digestive efficiency (we use the term to indicate the full range of measures which indicate the proportion of material or energy which is absorbed, assimilated or metabolised) (Castro et al., '89; Karasov, '90). Similarly one might suppose that predators would rarely encounter ecological constraints imposed by their digestion, such as restricted diet choice or limits to energy expenditure.

However, some observations suggest that there is variation in the efficiency with which predatory animals digest their food. We started this investigation by watching Egyptian Vultures (*Neophron percnopterus*) consuming Lion (*Panthera leo*) droppings. Some vultures spend much of their day watching Lion prides, just waiting for an animal to defecate and provide it with a meal (Houston, '88). This rather unsavoury foraging strategy is also curious. Why should a lion void faecal material from its gut if it still contains sufficient energy or nutrients to make it worthwhile for another species to eat it? Domestic cats are known to be about 10% less efficient at digesting food than domestic dogs (Kendall et al., '82), and this seems also to apply to wild cats (such as lions) and wild dog species (Houston, '88). Indeed, vultures have not been observed feeding on the dung of wild dogs, perhaps because it is not worth them doing so. This raises the question of whether some predatory species have constraints which prevent them from digesting food as efficiently as other species. In this paper we consider firstly whether there is evidence for variation in the apparent absorption efficiency of the various birds which feed on meat and fish. We then examine whether physiological and morphological traits, primarily gross gut morphology and retention time, are associated with observed variation in apparent absorption efficiency. We finally move on to assess the ecological constraints which might result in a diversity of digestion strategies, and apparently sub-maximal digestive efficiencies.

INTER-SPECIFIC VARIATION IN APPARENT ABSORPTION EFFICIENCY

Where variations in apparent absorption efficiency between species are likely to be small, as in the case of carnivorous and piscivorous birds, it is misleading to compare values which have been obtained in different experiments using different experimental designs. Small variations in the diet used, the experimental procedure,

or in the method of calculating digestive efficiency (see Miller and Reinecke, '84) could give considerable spurious variation.

However, in a few cases digestive efficiency has been measured on several species under the same conditions (Barton, '92; Jackson, '92; Barton and Houston, '93a; Brekke and Gabrielsen, '94). Table 1.1 shows that there is small, but statistically significant, variation between species in the efficiency with which they digest the same food types. The difference in percent efficiency between the most efficient and the least efficient species varies between experiments. For example Thick-billed Murre (*Uria lomvia*) and Black-legged Kittiwake (*Rissa tridactyla*) fed Capelin (*Mallotus villosus*) differ in efficiency by only 1.6% (although this difference is statistically significant) (Brekke and Gabrielsen, '94), whereas the difference between Blue Petrel (*Halobaena caerulea*) and King Penguin (*Aptenodytes patagonicus*) on a Squid (*Loligo vulgaris*) diet is as much as 11.6%. These differences could be of considerable ecological importance for bird species. In order to absorb an equal amount of energy, a species with a apparent absorption efficiency of 70% would have to catch and eat 12.5% more prey than a bird with an efficiency of 80%.

CAUSES OF VARIATION IN APPARENT ABSORPTION EFFICIENCY

Theoretical models of digestion derived from chemical reactor theory (Sibly, '81; Penry and Jumars, '87) predict the relationship between the digestive efficiency achieved by an animal and characteristics of its gastrointestinal structure and function. These relationships are summarised by Karasov ('96) as:

$$\text{digestive efficiency} \propto \left(\frac{\text{retention time} \cdot \text{reaction rate}}{\text{concentration} \cdot \text{digesta volume}} \right) \quad (1)$$

Concentration is the energy density (energy per unit volume) of the digesta.

Thus, if other parameters are held constant, an increase in retention time results in an increase in apparent absorption efficiency, whereas more rapid digestion results in a reduction in apparent absorption efficiency.

Table 1.1: Inter-specific variation in apparent absorption efficiency in experiments on seabirds and raptors

SPECIES	DIET	% DIGESTIVE EFFICIENCY (S.E.M.)	METHOD OF CALCULATION	REFERENCE
King Penguin <i>Aptenodytes patagonicus</i>	Squid (<i>Loligo vulgaris</i>)	79.9 (0.84)	TMEC* (endogenous energy losses estimated rather than measured)	1
Gentoo Penguin <i>Pygoscelis papua</i>	"	76.4 (1.88)		"
Rockhopper Penguin <i>Eudyptes chrysocome</i>	"	77.0 (1.95)		"
Sooty Albatross <i>Phoebastria fusca</i>	"	75.6 (0.53)		"
Blue Petrel <i>Halobaena caerulea</i>	"	68.3 (0.94)		"
White-chinned Petrel <i>Procellaria aequinoctialis</i>	"	76.6 (0.73)		"
Cape Gannet <i>Morus capensis</i>	"	72.2 (1.37)		"
King Penguin <i>Aptenodytes patagonicus</i>	Pilchard (<i>Sardinops ocellatus</i>)	70.9 (4.08)	TMEC* (endogenous energy losses estimated rather than measured)	"
Gentoo Penguin <i>Pygoscelis papua</i>	"	78.1 (1.42)		"
Rockhopper Penguin <i>Eudyptes chrysocome</i>	"	75.1 (2.37)		"
Sooty Albatross <i>Phoebastria fusca</i>	"	76.5 (0.71)		"
Blue Petrel <i>Halobaena caerulea</i>	"	77.4 (0.89)		"
White-chinned Petrel <i>Procellaria aequinoctialis</i>	"	75.6 (0.83)		"
Cape Gannet <i>Morus capensis</i>	"	75.5 (0.66)		"

King Penguin	<i>Aptenodytes patagonicus</i>	Prawn (<i>Penaeus indicus</i>)	72.9	TMEC* (endogenous energy losses estimated rather than measured)	“
Gentoo Penguin	<i>Pygoscelis papua</i>	“	78.2 (2.75)		“
Rockhopper Penguin	<i>Eudyptes chrysocome</i>	“	79.3 (2.11)		“
Sooty Albatross	<i>Phoebastria fusca</i>	“	78.4 (1.17)		“
Blue Petrel	<i>Halobaena caerulea</i>	“	74.5 (2.93)		”
White-chinned Petrel	<i>Procellaria aequinoctialis</i>	”	75.8 (0.76)		”
Cape Gannet	<i>Morus capensis</i>	“	70.8 (1.42)		“
Black-legged Kittiwake	<i>Rissa tridactyla</i>	Capelin (<i>Mallotus villosus</i>)	72.2 (0.7)	AMEC _N *	2
Thick-billed Murre	<i>Uria lomvia</i>	“	70.6 (0.6)		“
Black-legged Kittiwake	<i>Rissa tridactyla</i>	Arctic Cod (<i>Boreogadus saida</i>)	81.2 (0.4)	AMEC _N *	“
Thick-billed Murre	<i>Uria lomvia</i>	“	74.7 (0.9)		“
Western Honey Buzzard	<i>Pernis apivorous</i>	day-old chick	75.9	Dry Matter Digestibility [†]	3
Red Kite	<i>Milvus milvus</i>	“	82.0 (0.47)		“
Eurasian Sparrowhawk	<i>Accipiter nisus</i>	“	79.3		“
Eurasian Buzzard	<i>Buteo buteo</i>	“	81.6 (0.42)		“
Common Kestrel	<i>Falco tinnunculus</i>	“	80.2 (1.41)		“
Eurasian Hobby	<i>Falco subbuteo</i>	“	80.4		“
Peregrine	<i>Falco peregrinus</i>	“	78.9 (0.69)		“

*: TMEC = True Metabolisable Energy Coefficient (not nitrogen corrected)

AMEC_N = Apparent Metabolisable Energy Coefficient (nitrogen corrected)

see Miller and Reinecke (1984) for explanation of terms.

†: DMD = 1 - ((dry mass of faeces + dry mass of pellets)/dry mass of food)

References: 1: Jackson 1990; 2: Brekke & Gabrielsen 1994; Barton & Houston 1993a.

There is some experimental evidence that within a species there is a positive relationship between retention time and digestive efficiency. Omnivorous birds switched from a diet on which retention time is low, e.g. fruit, to a diet such as insects for which retention time tends to be higher, don't show an immediate change in retention time; rather their retention time gradually increases as they acclimate to the new diet. During this phase of increasing retention time their metabolisable energy coefficient tends to rise as well (Levey and Karasov, '92; Afik and Karasov, '95). Prop and Vulink, ('92) show that free living Barnacle Geese (*Branta leucopsis*) show seasonal variation in retention time, with concomitant variation in the efficiency of digestion of graminoids. In addition, Badgers (*Meles meles*) show a greatly increased retention time of digesta following a fast, and this is associated with much higher digestive efficiency (Harlow, '81). At an interspecific level, a negative relationship between retention time and digestive efficiency is evident across a large range of herbivores (Demment and Van Soest, '85). These differences are however associated with a very wide phylogenetic and body size range, and also with very major variation in the structure and function of the gut, and associated differences in the type of vegetable matter eaten. Such a relationship has not been shown to occur within ecologically and morphologically similar groups of species consuming similar foods. We therefore examined variation in digesta retention time, to see whether this explained the observed variation in apparent absorption efficiency in raptors.

APPARENT ABSORPTION EFFICIENCY IN RELATION TO RETENTION TIME

We measured apparent absorption efficiency and retention time in seven species of raptors. Tame birds from falconry collections were used in the digestion trials, so stress, which may affect digestion parameters, was not a factor in the experiments. Data from dissections indicate that gross gut morphology of these captive birds does not differ significantly from wild birds (Barton and Houston, '93a). Total faecal collections were made following single pulse meals. Meal sizes were sufficient to provide the metabolisable energy requirement for maintenance predicted by Kirkwood's ('81) equation. Apparent absorption efficiency was measured as:

$$\text{dry matter digestibility} = 1 - \left(\frac{\text{dry weight of faeces} + \text{dry weight of pellets}}{\text{dry weight of food}} \right) \quad (2)$$

Faecal collections were made every two hours, and retention time was measured as mean 14 hour retention time, following Warner ('81):

$$\text{mean retention time} = \frac{\sum_{i=1}^n m_i \cdot t_i}{\sum_{i=1}^n m_i} \quad (3)$$

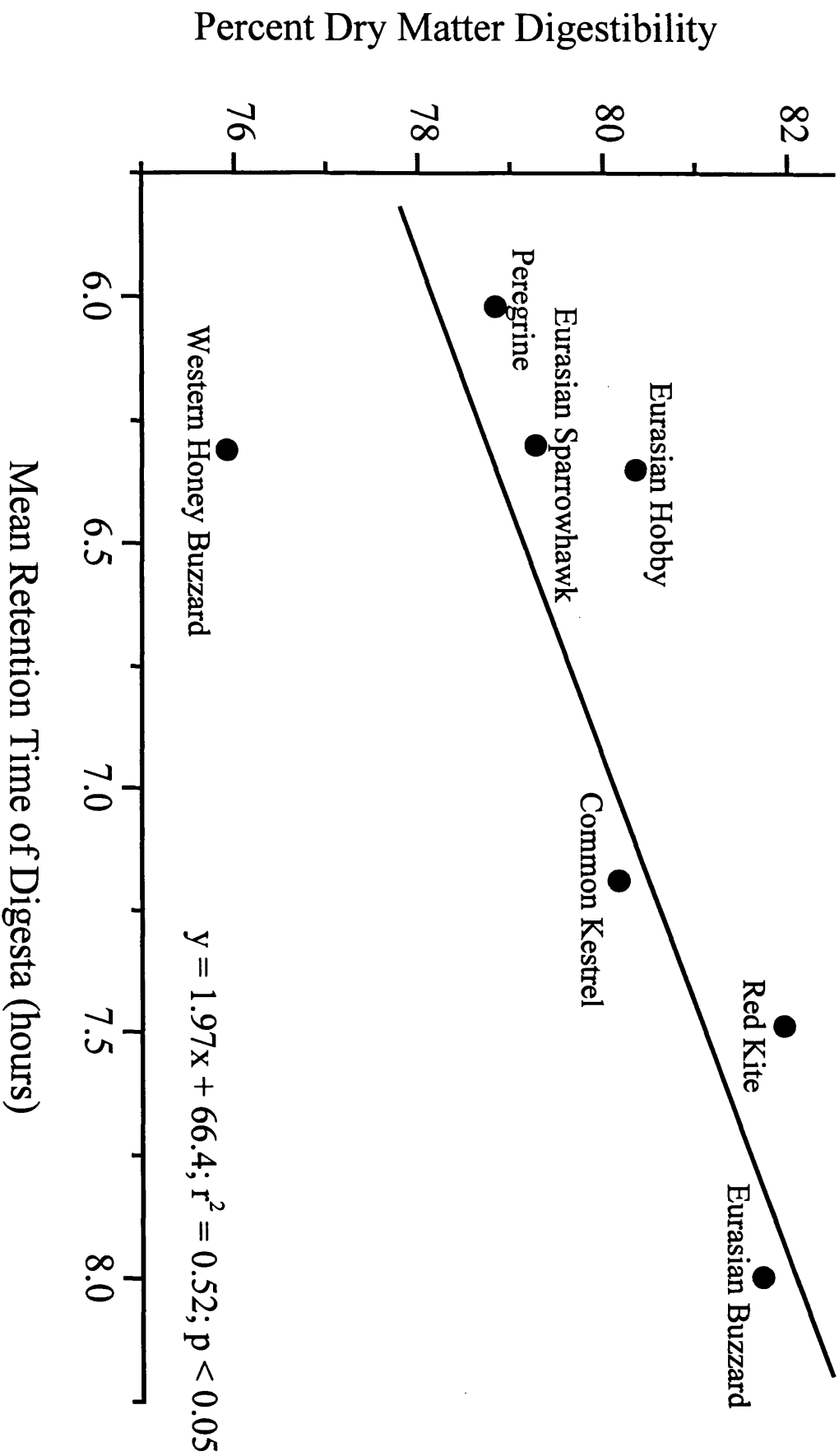
where m_i is the absolute amount of faeces produced at time interval t_i after feeding.

Figure 1.1 shows a positive relationship between apparent absorption efficiency and retention time. Variation in retention time explains about 50% of the variance in apparent absorption efficiency. Relatively large variation in retention time results in only small changes in apparent absorption efficiency: an increase of mean retention time from six to eight hours would result in a predicted increase in apparent absorption efficiency of only 78% to 82%. Western Honey Buzzard (*Pernis apivorous*) shows a rather low apparent absorption efficiency for its retention time, and this may be due to this species' rather specialised diet: in the wild it feeds mainly on Hymenoptera (Cramp and Simmons, '80). Adaptations of the gut to this diet may result in a lower than expected efficiency when fed vertebrate prey.

Further studies are under way on eight north Atlantic seabird species, to consider whether species which feed on fish show the same relationship. There is a strong suggestion that a similar interspecific relationship exists between retention time and apparent absorption efficiency for this group of species.

Fig 1.1: The relationship between apparent absorption efficiency and retention time in raptor species.

Sample sizes: Western Honey Buzzard 1; Peregrine 3; Eurasian Sparrowhawk 2;
Common Kestrel 5; Eurasian Hobby 2; Eurasian Buzzard 4; Red Kite 2.



CAUSES OF RETENTION TIME VARIATION

Mean retention time of digesta in the gut is determined by two factors: the length of the gut and the speed at which digesta travels along it.

$$\text{Hence: } \textit{retention time} = \frac{\textit{length of gut}}{\textit{rate of flow}} \quad (4)$$

Thus an animal can increase its rate of digestion either by shortening the gut, or by increasing the rate of flow of digesta, or by a combination of these two means. We used data from dissections of raptors, combined with retention time data, to determine which strategy is adopted.

To assess the relationship between small intestine length and gut retention time we used standardised residual small intestine lengths from linear regression of small intestine length on skeletal body size. A skeletal body size measure was preferred to body mass as a means of removing the confounding effect of size in the analyses (see Barton and Houston '94). Body mass reflects both structural size and nutrient reserve size of an animal (Piersma and Davidson '91), but nutrient reserve size is temporally variable, and is thus a potentially inaccurate measure. In intraspecific studies, it is normal to use the factor loadings on the first principal component axis of a Principal Components Analysis on measurements of several body parts to estimate skeletal body size (Rising and Somers '89). However, when PCA was performed separately for each species on the skeletal variables measured in this study, different variables proved to be important in determining skeletal body size (shown by very different factor loadings on the first principal component axis) for different species. Therefore we used the two skeletal variables which had consistently high loadings on the first principal component axis for all species - keel length and diagonal length (distance from base of sternum to distal point of coracoid) - to calculate skeletal body size as:

$$\textit{keel} \cdot \textit{diagonal}^{0.5} \quad (5)$$

The residual small intestine lengths are independent of body size (Pearson Correlation $r = 0.14$, $p > 0.1$). Figure 1.2 indicates a strong relationship between residual small intestine length and gut retention time. It appears that rapid digestion in raptors is associated with shortening of the absorptive section of the gut. The

resultant effect on apparent absorption efficiency is illustrated in Figure 1.3, which shows that residual small intestine length is inversely related to apparent absorption efficiency. Species with relatively short small intestines, controlling for body size, tend to have, as predicted, rather low digestive efficiencies.

We estimated rate of flow of digesta as small intestine length divided by mean retention time. This is clearly a rather crude approximation, since rates of gastric evacuation of food may vary. In addition reflux of intestinal contents into the stomach may occur in some species (Duke et al., '97). Reduced major axis regression indicates that rate of flow of digesta is positively related to small intestine length (flow rate (cm.hour⁻¹) = 1.5 + small intestine length (cm) x 0.12; $F_{1,5} = 27.9$, $p < 0.001$). Thus rate of flow increases as gut length increases. This would seem to imply that in fact there is no effect of gut length on retention time. However, the relationship between gut length and flow rate is not isometric; gut length increases are not fully compensated by flow rate increases.

In order to assess whether flow rate variation also causes variation in retention time, we analysed the standardised residuals of species' values on the flow rate - gut length regression. This reveals that species with *relatively* fast rates of digesta flow, that is with flow rates exceeding the predicted value for their gut length, tend to have short digesta retention times (Spearman-rank correlation between standardised residual flow rate and gut retention time $r_s = -0.86$; $p = 0.01$; $n = 7$).

Thus the observed variation in retention time of digesta is explained by a combination of gut length variation, and flow rate variation. Species use both mechanisms in order to reduce or increase their gut retention times.

Fig 1.2: The relationship between small intestine length and retention time in raptor species (modified from Barton and Houston '93b).

Sample sizes for small intestine length: Western Honey Buzzard 1; Peregrine 16; Eurasian Sparrowhawk 89; Common Kestrel 24; Eurasian Hobby 1; Eurasian Buzzard 53; Red Kite 9. Sample sizes for retention time as for Fig 1.1.

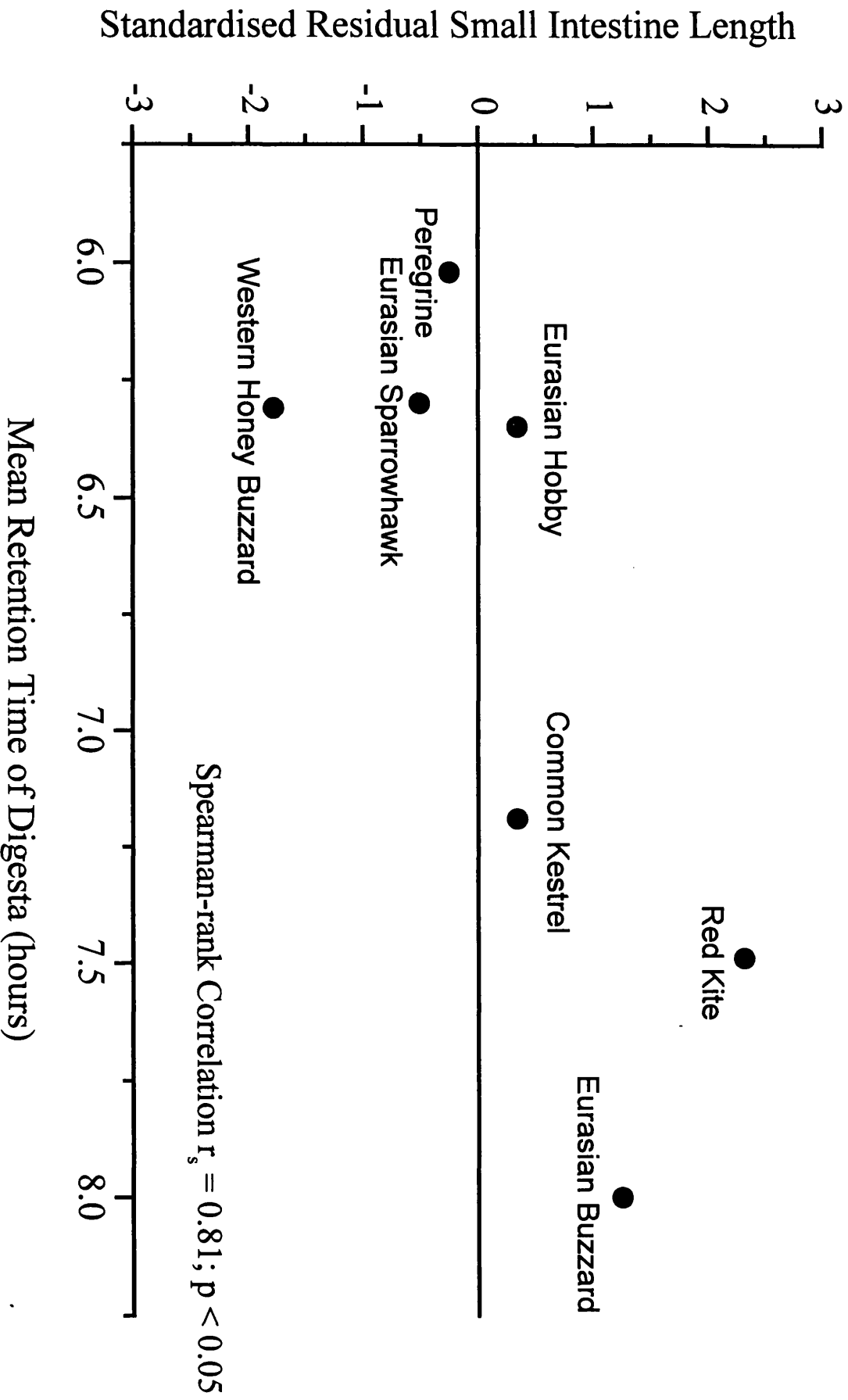
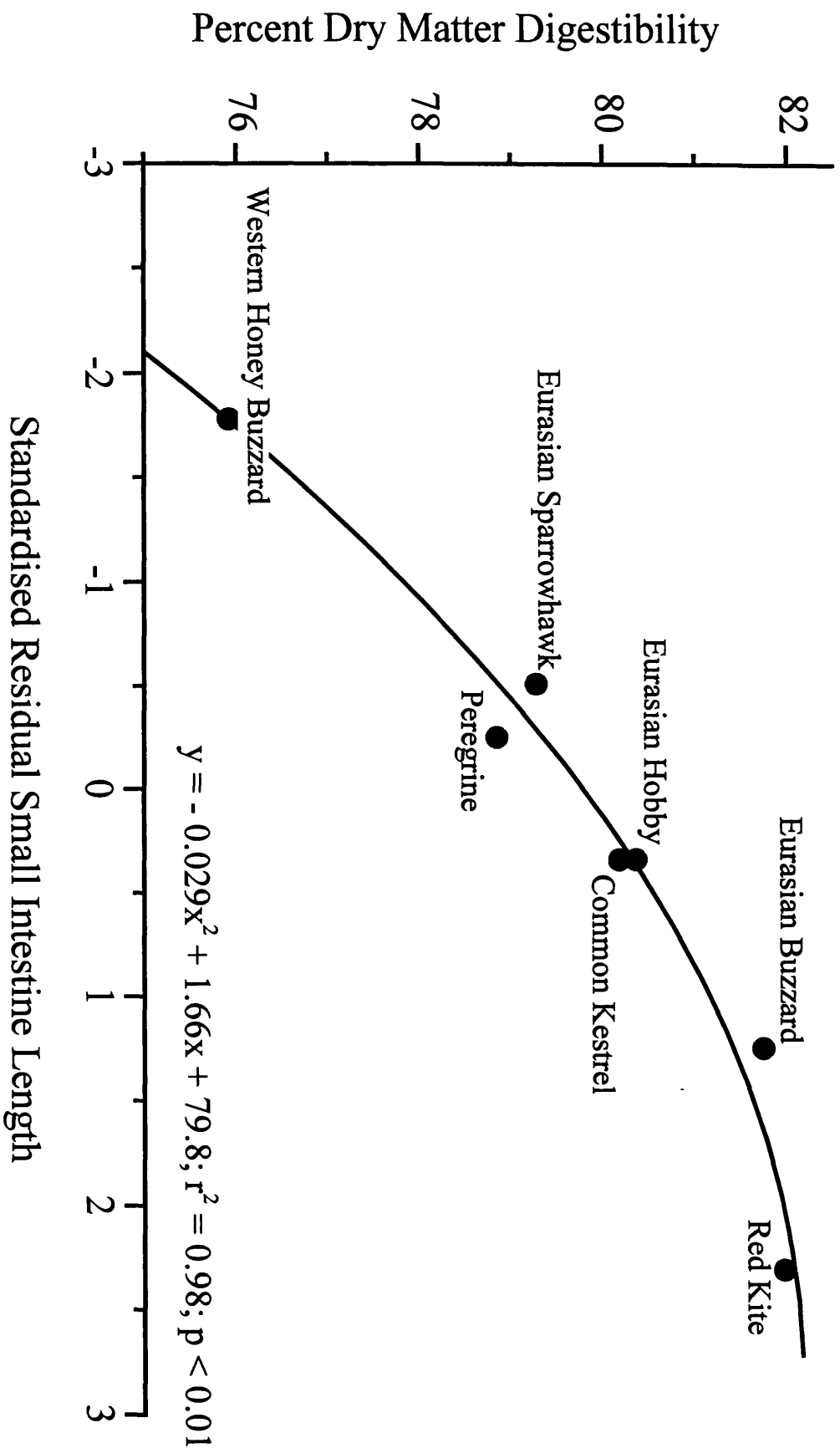


Fig 1.3: The relationship between small intestine length and apparent absorption efficiency in raptor species (modified from Barton and Houston '93a).

Sample sizes as for Figs 1.1 and 1.2.



ECOLOGICAL CONSTRAINTS ON DIGESTION PARAMETERS

We can conclude from the data already presented that not all meat eating species digest food with equal efficiency. Furthermore there is evidence that reduced apparent absorption efficiency in some species is a result of rapid digestion, caused by two factors - rapid movement of digesta and possession of a relatively short gut. There may be selective pressures on some species which cause them to evolve digestive systems that digest meat or fish more rapidly, but less efficiently, than other species. What might these selection pressures be ?

Predatory Strategy

We suggest that the reason why some species appear to adopt a strategy of rapid digestion and small gut - resulting in lowered apparent absorption efficiency - is due to the mass savings that can be obtained. Recent work has focused on the adaptive significance of body mass regulation in small birds (Witter and Cuthill, '93). It has been suggested that, while large fat deposits are beneficial to individuals because they reduce the risk of starvation, they also have a cost: the mass of fat reduces flight performance, thus making the bird more susceptible to predation (Metcalf and Ure '95), and also increasing the energy expenditure in flight (Pennycuik '89; Norberg '90). In a similar way, it is possible that birds are presented with a retention time - apparent absorption efficiency trade-off. Fast digestion results in rapid mass loss due to defecation after a meal. A small gut, besides being a means to achieve rapid digestion, also serves to reduce mass carried, both because of its low tissue mass and because of its low digesta capacity. In some circumstances the benefits of mass saving may outweigh the costs, which are low apparent absorption efficiency. The strategies of rapid digestion and/or small gut would be selected, even though they led to poor apparent absorption efficiency, if the outcome of the trade-off was an overall greater rate of prey capture, reduced energy expenditure, or reduced time needed for foraging.

In species which pursue active prey, selection might be expected to favour reduction in any non-muscular component of body mass. Acceleration, turning speed, agility and maximum velocity in flight are all mass dependent (Andersson and Norberg, '81). A bird which reduces the size of the digestive tract, thus lowering tissue mass

and mass of digesta carried, and/or which increases the rate of food throughput can more quickly reduce its body mass and regain maximum predatory efficiency following a meal.

A comparative approach is used to test the idea that short gut and rapid digestion are a result of selection for mass minimisation. We predict that birds which pursue active prey, such as small birds caught in flight, and which therefore benefit greatly from mass reduction, will tend to adopt a strategy of “rapid but inefficient” digestion. Species which search over large areas for carrion or slow moving terrestrial prey, and which drop onto prey from above without an extensive chase, will have evolved a “slow and efficient” strategy. We divided raptor species into two categories: “Searchers”, such as Eagles, Buzzards and Kites, are those species which feed predominantly on mammals and carrion, and do not usually require active pursuit of prey. “Pursuers” are species such as Eurasian Sparrowhawk (*Accipiter nisus*), Northern Goshawk (*Accipiter gentilis*), and Peregrine (*Falco peregrinus*) which have more than 75% avian prey in their diet (Brown, ‘78). There does indeed appear to be a relationship between foraging type and digestive strategy in raptors.

Figure 1.4 shows the outcome of an ANCOVA with small intestine length as dependent variable, skeletal body size as covariate and predatory strategy as a factor. “Searchers” have significantly longer small intestines than “pursuers”. “Searchers” also have shorter mean retention time of digesta than “pursuers” (Mann-Whitney $U=6$; $n=6$; $p<0.05$). For instance the Peregrine, with a body mass of 711 g has a mean small intestine length of 836 mm and a mean retention time of 6.02 hours, whereas the Eurasian Buzzard (*Buteo buteo*), body mass 719 g, has a mean small intestine length of 1011 mm and a mean retention time of 8.00 hours.

The skeletal body size measure was not affected by shape differences between pursuers and searchers. Skeletal size was estimated from body trunk variables, which are less likely to be affected by predatory strategy than tail and wing length measures. Furthermore an Analysis of Covariance showed that, for a given body mass, there was no difference between pursuers and searchers in estimated skeletal body size (body mass regression $F_{1,13} = 70.6$, $p<0.001$; predatory strategy $F_{1,13} = 0.21$, n.s.).

Although our preliminary analysis of work done on north Atlantic seabirds suggests that there is a negative correlation between metabolisable energy coefficient and retention time, for this group of birds the observed relationship cannot so readily be explained by variations in foraging strategy. The ecological factors which might determine which strategy is favoured in fish eating birds are perhaps more complex and variable than in raptors. Birds of prey are mostly territorial, and so virtually all species, regardless of predatory strategy, have only a short distance to carry the food back to the nest (Cramp and Simmons, '80). Most fish eating birds forage from a central colony, but foraging ranges, meal frequencies, and flight costs vary dramatically between different members of the guild (Cramp and Simmons, '77; Cramp and Simmons, '83; Cramp, '85; Croxall, '87; Phillips in press). In seabirds a mass saving, inefficient digestive strategy may be favoured if the energy costs of commuting between colony and feeding ground are particularly high. However, the daily energy costs of commuting may be high for different reasons in different species: some may have very high rates of flight energy expenditure (e.g. Alcidae, (Pennycuik '89)), some make very frequent foraging trips (e.g. Laridae, (Cramp & Simmons '83)), some may make very long range foraging trips (e.g. Procellariiformes, (Warham, '96)). In addition to the variable effects of payload on flight costs, and hence overall energetics, there may also be a direct effect of payload on prey capture rates. As with the raptors, this might primarily be expected to affect pursuit foragers. However, pursuit foraging seabirds operate under water, and the effects of carrying extra mass on underwater pursuit ability have not been determined; it is unclear whether mass reduction would enhance prey capture rates of species that catch fish in underwater pursuit in the same way that it would for aerial predators of birds. Thus the interaction between the different costs and benefits of carrying mass are much more complex in seabirds than in raptors, and less amenable to simple predictions.

Because of these difficulties in predicting which seabird species will be selected for rapid digestion and which for slower digestion, we developed a model based on time-energy budgets to quantify the effects on the daily energy expenditure of variations in retention time (Hilton et al. *in prep.*). We developed a time-energy budget for the Common Murre (*Uria aalge*), which shows the fastest and least efficient digestion of

eight north Atlantic seabird species (G. Hilton *unpubl. data*). We used our measured values for apparent absorption efficiency and retention time of Common Murres to predict the mass trajectory of the bird during a foraging cycle. We then changed apparent absorption efficiency and retention time to that of a Northern Fulmar (*Fulmarus glacialis*), which shows slow but efficient digestion (G. Hilton *unpubl. data*). Figure 1.5 shows that immediately after the meal the bird with the short retention time (“rapid digester”) weighs more than the bird with the long retention time (“slow digester”). This is because the lower efficiency of rapid digestion means that the bird must eat more food in order to assimilate the same amount of metabolisable energy. However, within two hours of the end of the feeding bout, the rapid digester is lighter than the slow digester by virtue of its greater excretion rate. Thus the temporal distribution of feeding and commuting activity determines which strategy is favoured for mass minimisation.

Fig 1.4: The relationship between foraging mode and small intestine length in raptor species (modified from Barton and Houston '94).

species: 1 = Common Kestrel (*Falco tinnunculus*) (n=24); 2 = Hen Harrier (*Circus cyaneus*) (n=4); 3 = Rough-legged Buzzard (*Buteo lagopus*) (n=1); 4 = Eurasian Buzzard (*Buteo buteo*) (n=53); 5 = Tawny Eagle (*Aquila rapax*) (n=1); 6 = Red Kite (*Milvus milvus*) (n=9); 7 = Golden Eagle (*Aquila chrysaetos*) (n=6); 8 = Eleonora's Falcon (*Falco eleonora*) (n=1); 9 = Merlin (*Falco columbarius*) (n=3); 10 = Eurasian Sparrowhawk (*Accipiter nisus*) (n=89); 11 = Eurasian Hobby (*Falco subbuteo*) (n=1); 12 = Lanner Falcon (*Falco biarmicus*) (n=2); 13 = Northern Goshawk (*Accipiter gentilis*) (n=49); 14 = Peregrine (*Falco peregrinus*) (n=16); 15 = Saker Falcon (*Falco cherrug*) (n=1).

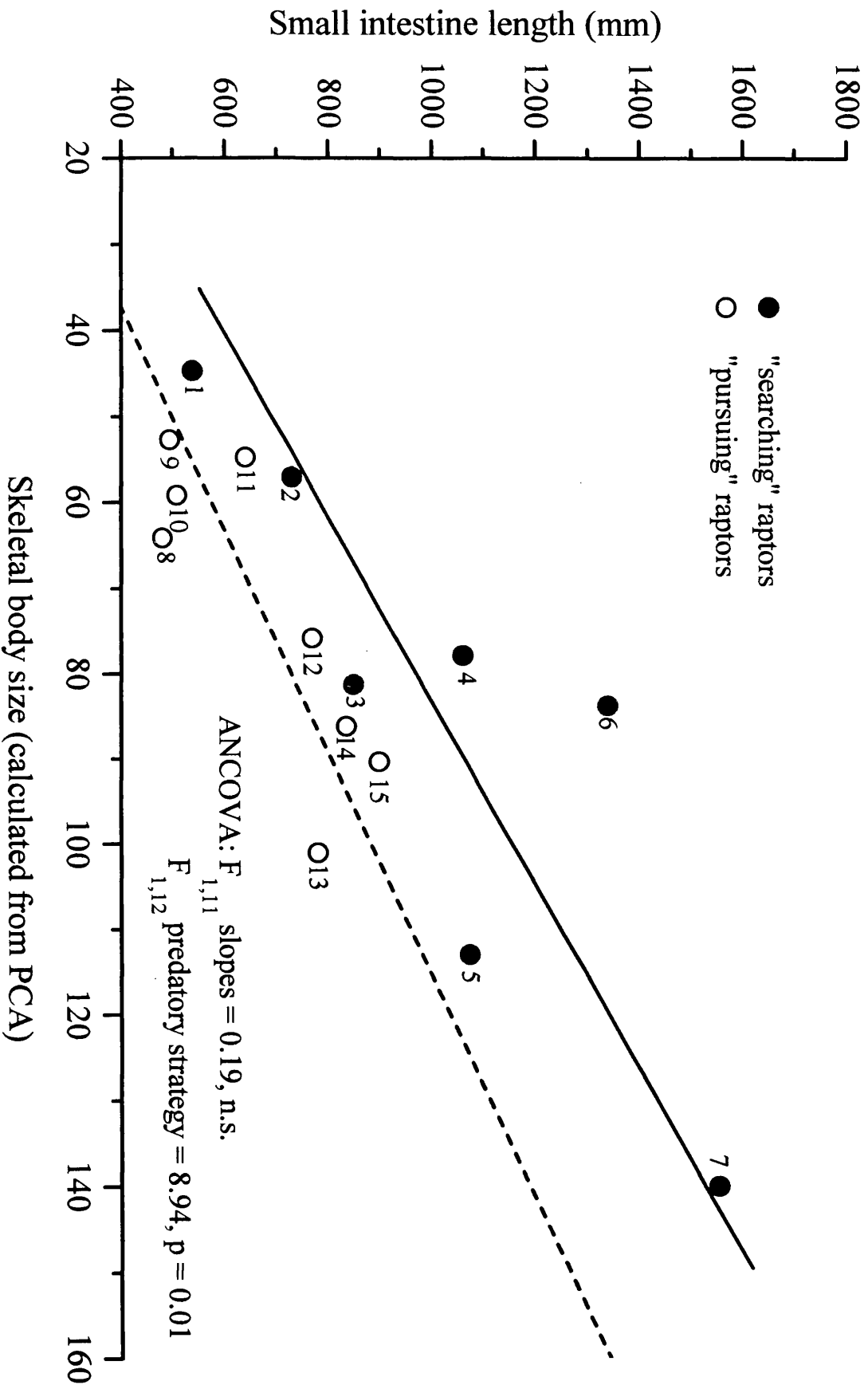
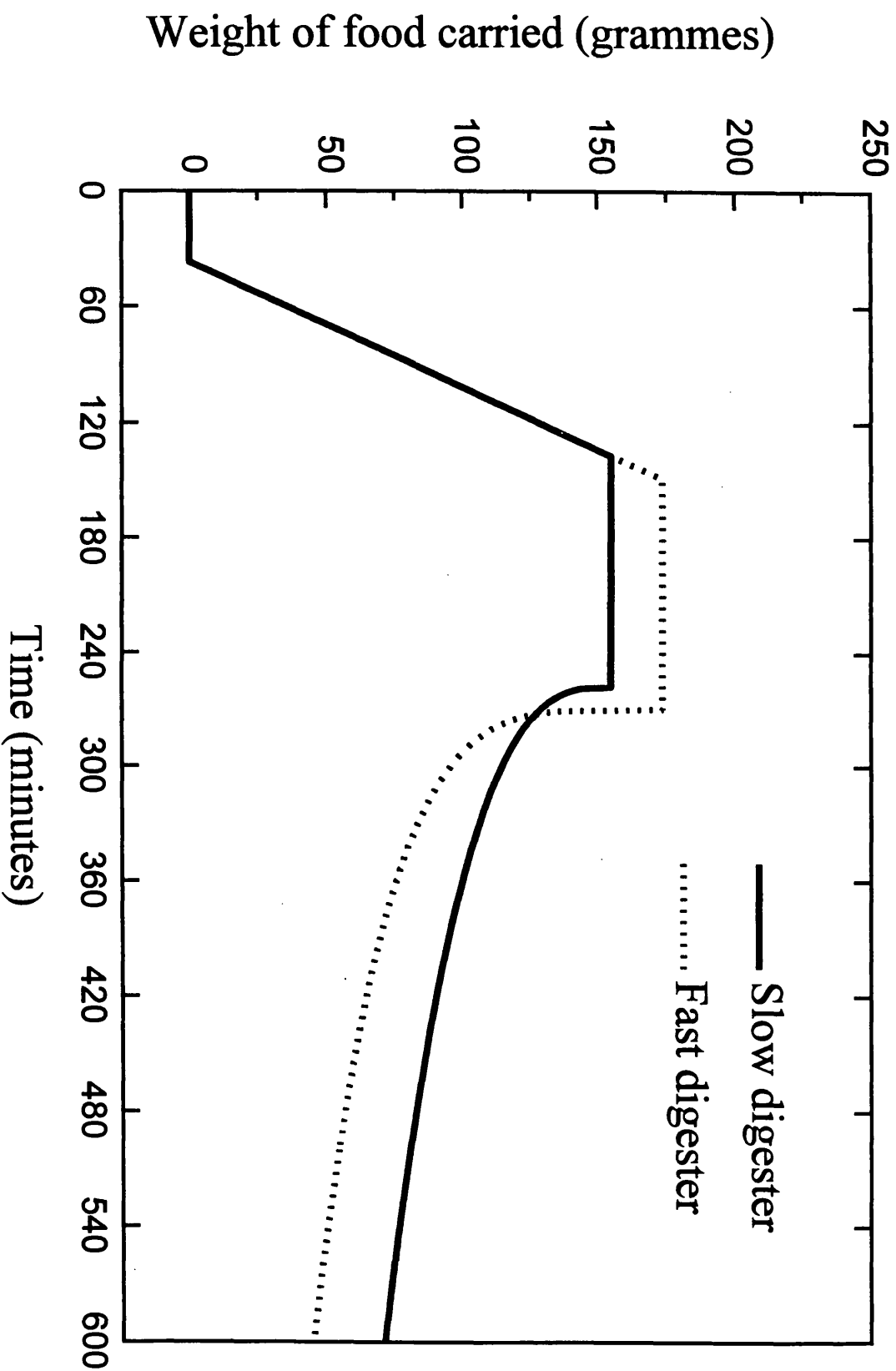


Fig 1.5: The results of a modelling exercise showing mass trajectories of a “fast digester” and a “slow digester” Common Murre following a meal.

"fast digester" represents mass loss of a bird showing the observed retention time for Common Murres. "slow digester" represents mass loss of a bird showing the observed retention time for Northern Fulmar.



Ecological consequences of variation in digestive strategy

Variation in apparent absorption efficiency could have a profound influence on prey selection and feeding niche width. Species with low apparent absorption efficiency may be restricted to feeding on high quality diets, whereas species with high apparent absorption efficiency are able to occupy a broader feeding niche, including low quality food types.

Barton and Houston ('93a) examined the body mass trajectories of a low efficiency species - the Peregrine, and a high efficiency species - the Eurasian Buzzard, when fed diets of contrasting quality. The diets were Rabbit meat (*Oryctolagus cuniculus*), which has a low fat content, and Pigeon meat (*Columba livia*) which has a high fat content. Meal sizes were calculated to meet maintenance requirements, estimated on the basis of body mass (Kirkwood, '81). Peregrines lost an average 5% of body mass over an eight day period when fed rabbit, whereas Eurasian Buzzards gained an average 2.8% over the same period. However, on a diet of pigeon both species were able to maintain body mass. It therefore seems likely that Peregrines and other low efficiency species will tend to avoid low quality prey to a far greater extent than will high efficiency species. This concurs with anecdotal observations of falconers that Peregrines are unable to maintain mass on low quality meat, even when fed *ad libitum*.

In some circumstances an inefficient digester can simply increase its food intake to deal with reduced food quality, and thereby meet its energy requirements. However this response could fail (1) if the apparent absorption efficiency of species with inefficient digestion gets even lower relative to species with efficient digestion as food quality declines and gut retention time decreases. At present there are few data that bear on this question. (2) If the cost of carrying the extra mass associated with eating large amounts of a poor quality diet is disproportionately large. For instance foraging efficiency may be greatly diminished by extra mass. The adverse effect on flight ability of a given increase in body mass can be quantified (Andersson and Norberg, '81). However pursuit and capture of avian prey is an all-or-nothing event. The proportion of attacks which result in prey capture is often very low in pursuit hunting raptors (Temeles, '85). For instance percent of attacks on avian prey which

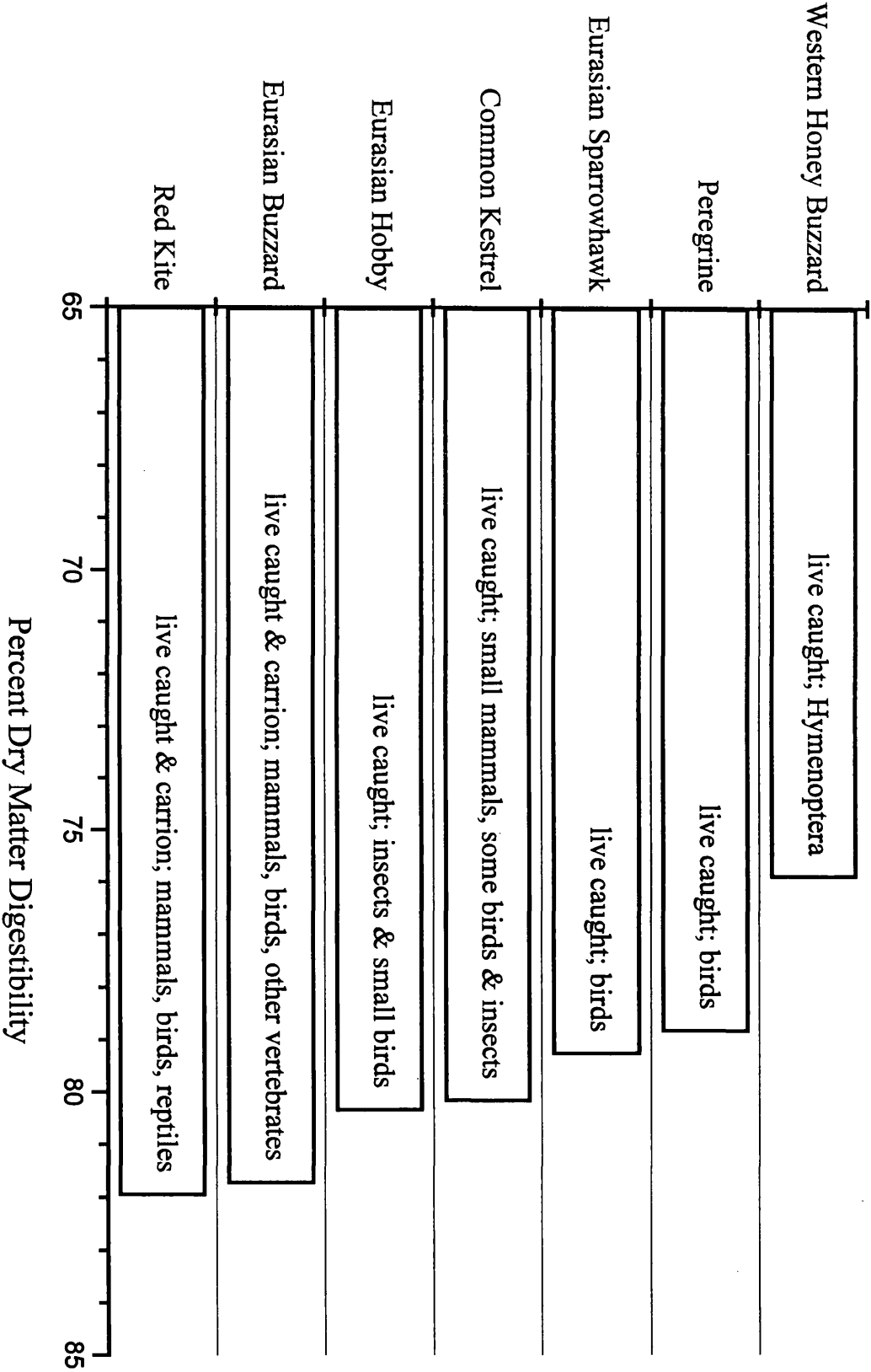
were successful has been measured as 5% for Northern Goshawks (Kenward, '82), 5% for Merlins (*Falco columbarius*) (Rudebeck, '51) and 7.5% for Peregrines (Rudebeck, '51). When success rate is as low as this, only a slight deterioration in flying ability may produce a disproportionate decline in prey capture rate.

Analysis of the diets of the study species in the wild supports the suggestion that inefficient digestion is associated with a restricted, mainly high quality diet. Among raptors, species which we have found to have efficient digestion, such as Red Kite (*Milvus milvus*) and Eurasian Buzzard occupy broad feeding niches. They frequently take very low quality diets, such as carrion and invertebrates such as earthworms (Cramp and Simmons, '80). By contrast, species which we find to have relatively low apparent absorption efficiency, such as Peregrine and Eurasian Sparrowhawk, are notable for the restricted range of their diet, consuming almost entirely live-caught avian prey (Cramp and Simmons, '80), which has comparatively high calorific value. Figure 1.6 illustrates this association between diet and apparent absorption efficiency. A further complication may arise for the latter group of species: the easiest avian prey to catch may well be malnourished individuals which show poor escape ability. However, the reduced nutritional value of starving birds may make them undesirable as prey. Taylor et al. ('91) found that American Kestrels (*Falco sparverius*) were unable to maintain mass when fed starved passerine prey, despite greatly increasing their food intake.

Initial indications are that a similar association between apparent absorption efficiency and normal diet choice occurs in seabirds: The Auk species which we examined appear to have rather inefficient digestion, and are notable for being predominantly piscivorous, especially selecting oily fish of high calorific value such as Clupeids (Bradstreet and Brown, '85, Cramp, '85;). Gulls, Skuas (Stercorariidae) and Procellariiformes have higher digestive efficiencies and also have more varied diets, including lower quality invertebrate prey (Cramp and Simmons, '77; Cramp and Simmons, '83; Warham, '96).

Fig 1.6: Apparent absorption efficiency of raptor species in relation to their typical natural diets.

Apparent absorption efficiency values obtained from birds eating day-old chicks (Barton & Houston '93a). Sample sizes as for Fig 1.1.



LITERATURE CITED

- Afik, D. and W.H. Karasov (1995) The trade-offs between digestion rate and efficiency in warblers and their ecological implications. *Ecology* 76: 2247-2257.
- Andersson, M. and R.A. Norberg. (1981) Evolution of sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biol. J. Linn. Soc.* 15: 105-130.
- Ankney, C.D. (1977) Feeding and digestive organ size in breeding Lesser Snow Geese. *Auk*: 94: 275-282.
- Barnes, G.G. and V.G. Thomas (1987) Digestive organ morphology, diet and guild structure of North American Anatidae. *Can. J. Zool.* 65: 1812-1817.
- Barton, N.W. H. (1992) Morphological adaptation and digestion in relation to raptor feeding ecology. 1-163.(Unpubl. PhD Thesis, University of Glasgow).
- Barton, N.W.H. and D.C.Houston (1993a) A comparison of digestive efficiency in birds of prey. *Ibis* 135: 363-371.
- Barton, N.W.H. and D.C.Houston (1993b) The influence of gut morphology on digestion time in raptors. *Comp. Biochem. Physiol* 105A: 571-578.
- Barton, N.W.H. and D.C. Houston (1994) Morphological adaptation of the digestive tract in relation to feeding ecology of raptors. *J. Zool. Lond.* 232: 133-150.
- Bradstreet, M.S.W. and R.G.B. Brown (1985) Feeding ecology of the Atlantic Alcidae. In: *The Atlantic Alcidae; The Evolution, Distribution and Biology of the Auks Inhabiting the Atlantic Ocean and Adjacent Water Areas*. D.N. Nettleship and T.R. Birkhead, eds. Academic Press: London.
- Brekke, B. and G.W. Gabrielsen (1994) Assimilation efficiency of adult Kittiwakes and Brunnich's Guillemots fed Capelin and Arctic Cod. *Polar Biol.* 14: 279-284.
- Brown, L.H. (1978) *British Birds of Prey*, Collins: London.
- Castro, G.N. Stoyan and J.P. Myers (1989) Assimilation efficiency in birds: a function of taxon or food type ? *Comp. Biochem. Physiol.* 92A: 271-278.

- Cramp, S (1985) Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic; Volume 4: Terns to Woodpeckers, Oxford University Press, Oxford.
- Cramp, S. and K.E.L. Simmons (1977) Handbook of the birds of Europe the Middle East and North Africa: The birds of the Western Palearctic; Volume 1: Ostrich to Ducks, Oxford University Press, Oxford.
- Cramp, S and K.E.L. Simmons (1980) Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic; Volume 2: Hawks to Bustards, Oxford University Press, Oxford.
- Cramp, S and K.E.L. Simmons (1983) Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic; Volume 3: Waders to Gulls, Oxford University Press, Oxford.
- Croxall, J.P. (ed) (1987) Seabirds: feeding ecology and role in marine ecosystems, Cambridge University Press, Cambridge.
- Demment, M.W. and P.J. Van Soest (1985) A nutritional explanation for body-size patterns of ruminant and non-ruminant herbivores. *Am Nat.* 125: 641-672.
- Diamond, J.M., W.H. Karasov, D. Phan, and F.L. Carpenter (1986) Digestive physiology is a determinant of foraging bout frequency in Hummingbirds. *Nature* 320: 62-63.
- Duke, G.E. (1986) Alimentary canal: secretion and digestion, special digestive functions and absorption. In: *Avian Physiology* 4th edition, P.D. Sturkie, ed. Springer-Verlag, New York.
- Duke, G.E., J. Reynhout, A.L. Tereick, A.R. Place, and D.M. Bird (1997) Gastrointestinal morphology and motility in American Kestrels receiving high or low fat diets. *Condor* 99: 123-131.
- Grajal, A., S.D. Strahl, R. Parra, M.G. Dominguez, and A. Neher (1989) Foregut fermentation in the Hoatzin, a neotropical leaf-eating bird. *Science* 245: 1236-1238.
- Harlow, H.J. (1981) Effect of fasting on rate of food passage and assimilation efficiency in badgers. *J. Mammal.* 62: 173-177.

Houston, D.C. (1988) Digestive efficiency and hunting behaviour in cats, dogs and vultures. *J. Zool. Lond.* 216: 603-605.

Jackson, S. (1990) Seabird digestive physiology in relation to foraging ecology, PhD. Diss., Univ. of Cape Town, Rondebosch, South Africa.

Jackson, S. (1992) Do seabird gut sizes and mean retention times reflect adaptation to diet and foraging method? *Physiological Zoology* 65, 674-697.

Karasov, W.H. (1990) Digestion in birds: chemical and physiological determinants and ecological implications. *Stud. Avian. Biol.* 13: 391-415.

Karasov, W.H. (1996). Digestive plasticity in avian energetics and feeding ecology. In: *Avian Energetics and Nutritional Ecology*, C. Carey ed., Chapman and Hall, New York.

Karasov, W.H. and I.D. Hume (1996) Vertebrate gastrointestinal system. In: *Handbook of Comparative Physiology*, W. Dantzler ed., American Physiological Society, Washington D.C..

Karasov, W.H. and D.J. Levey (1990) Digestive system trade-offs and adaptations of frugivorous passerine birds. *Physiol. Zool.* 63: 1248-1270.

Kehoe, F.P. and C.D. Ankney (1985) Variation in digestive organ size among five species of diving ducks. *Can J. Zool.* 63: 2339-2342.

Kendall, P.T., D.W. Holme, and P.M. Smith (1982) Comparative evaluation of net digestive and absorptive efficiency in dogs and cats fed a variety of contrasting diet types. *J. Small Anim. Pract.* 23: 577-587.

Kenward, R.E. (1982) Goshawk hunting behaviour and range size as a function of food and habitat availability. *J. Anim. Ecol.* 51: 69-80.

Kenward, R.E. and R.M. Sibly (1977) A woodpigeon (*Columba palumbus*) feeding preference explained by a digestive bottleneck. *J. Appl. Ecol.* 14: 815-826.

Kirkwood, J.K. (1981) Maintenance energy requirements and rate of weight loss during starvation in birds of prey. In: *Recent Advances in the Study of Raptor Diseases*, J.E. Cooper and A.G. Greenwood, eds., Chiron. Publications, Keighley, U.K..

- Kirkwood, J.K. (1985) Food requirements for deposition of energy reserves in raptors. In: Conservation Studies on Raptors: Proceedings of the ICBP World Conference on Birds of Prey, 1982, I. Newton and R.D. Chancellor, eds., International Council for Bird Preservation, Cambridge, U.K..
- Lee, W.B. and D.C. Houston (1993) The effect of diet quality on gut anatomy in British voles (Microtinae). *J. Comp. Physiol. B* 163: 337 - 339.
- Lee, W.B. and D.C. Houston (1995) The rate of change of gut anatomy in voles in relation to diet quality. *J. Zool., Lond.* 236: 341 - 345
- Leif, A.P. and L.M. Smith (1993) Winter diet quality, gut morphology and condition of Northern Bobwhite and Scaled Quail in West Texas. *J. Field Ornithol.* 64: 527-538.
- Leopold, S. (1953) Intestinal morphology of gallinaceous birds in relation to food habits. *J. Wildl. Manage.* 17: 197-203.
- Levey, D.J. and W.H. Karasov (1989) Digestive responses of temperate birds switched to fruit or insect diets. *Auk* 106: 675-686.
- Levey, D.J. and W.H. Karasov (1992) Digestive modulation in a seasonal frugivore, the American Robin (*Turdus migratorius*). *Am. J. Physiol.* 262: G 711-G 718.
- McLelland, J. (1979) Digestive System. In: Form and Function in Birds, Volume 1, A.S. King and J. McLelland, eds., Academic Press, London.
- McNeill Alexander, R. (1993) The relative merits of foregut and hindgut fermentation. *J. Zool. Lond.* 231: 391-401.
- Metcalf, N.B. and S.E. Ure (1995) Diurnal variation in flight performance and hence potential predation risk in small birds. *Proc. R. Soc. Lond. B* 261: 395 - 400.
- Miller, M.R. (1975) Gut morphology of Mallards in relation to diet quality. *J. Wildl. Manage.* 39: 168-173.
- Milton, K. (1981) Food choice and digestive strategies of two sympatric primate species. *Am. Nat.* 117: 476-495.
- Newton, I. (1979) Population ecology of raptors, T & A.D. Poyser, Hertfordshire, U.K..

- Norberg, U. (1990) How a long tail and changes in mass and wing shape affect the cost for flight in animals. *Funct. Ecol.* 9: 48 - 54
- Pennycuik, C.J. (1987) Flight of auks (alcidae) and other northern seabirds compared with southern procellariiformes: ornithodolite observations. *J. Exp. Biol.* 128: 335 - 347.
- Pennycuik, C.J. (1989) Bird flight performance: a practical calculation manual, Oxford University Press, Oxford, U.K..
- Penry, D.L. and P.A. Jumars (1987) Modelling animal guts as chemical reactors. *Am. Nat.* 129: 69-96.
- Phillips, R.A. (1996) N. Ratcliffe and H.T. Riley (in press) Factors influencing the foraging range and marine distribution of U.K. seabirds with an evaluation of possible marine extensions to Special Protection Areas in Scotland, Scottish Natural Heritage Research and Advisory Series, Scottish Natural Heritage, Edinburgh, U.K..
- Place, A.R. and D.D. Roby (1986) Assimilation and deposition of dietary fatty alcohols in Leach's Storm Petrel *Oceanodroma leucorhoa*. *J. Exp. Zool.* 240: 149-161.
- Roby, D.D., A.R. Place, and R.E. Ricklefs (1986) Assimilation and deposition of wax esters in planktivorous seabirds. *J. Exp. Zool.* 238: 29-41.
- Piersma, T. and Davidson, N.C. (1991) Confusions of mass and size. *Auk* 108: 441-444.
- Prop, J. and T. Vulink (1992) Digestion by Barnacle Geese in the annual cycle: the interplay between retention time and food quality. *Funct. Ecol.* 6: 180-189.
- Pulliainen, E. and P. Tunkkari (1983) Seasonal changes in the gut length of the Willow Grouse (*Lagopus lagopus*) in Finnish Lapland. *Ann. Zool. Fennici* 20: 53-56.
- Rising, J.D. and Somers, K.M. (1989) The measurement of overall body size in birds. *Auk* 106: 666-674.
- Rudebeck, G. (1951) The choice of prey and modes of hunting of predatory birds with special reference to their selective effort. *Oikos* 2: 65-88.

Sedinger, J.S., R.G. White, F.E. Mann, F.A. Buris, and R.A. Kedrowski (1989) Apparent metabolisability of alfalfa components by yearling Pacific Black Brant. *J. Wildl. Manage.* 53: 726-734.

Sibly, R.M. (1981) Strategies of digestion and defaecation. In: *Physiological Ecology: an evolutionary approach to resource use*, C.R. Townsend and P. Calow eds., Blackwell Scientific Publications, Oxford.

Taylor, R.L., S.A. Temple, and D.M. Bird (1991) Nutritional and energetic implications for raptors consuming starving prey. *Auk* 108: 716-719.

Temeles, E.J. (1985) Sexual size dimorphism of bird-eating hawks: the effect of prey vulnerability. *Am. Nat.* 125: 485-499.

Van Soest, P.J. (1982) Nutritional ecology of the ruminant, O. and B. Brooks, Corvallis, Oregon.

Warham, J. (1996) The behaviour, population biology and physiology of the petrels, Academic Press, London.

Warner, A.C. I. (1981) Rate of passage of digesta through the gut of mammals and birds. *Nutr. Abs. Rev. Ser. B* 51: 789-820.

Weiner, J. (1992) Physiological limits to sustainable energy budgets in birds and mammals: ecological implications. *Trends Ecol. Evol.* 7: 384-388.

Witter, M.S. and I.J. Cuthill (1989) The ecological costs of avian fat storage. *Phil. Trans. R. Soc. Lond. B.* 340: 73-92.

chapter 2

A COMPARATIVE STUDY OF DIGESTION IN NORTH ATLANTIC SEABIRDS

submitted for publication in *Journal of Avian Biology* as:

Hilton, G.M., R.W. Furness and D.C. Houston. A comparative study of digestion in North Atlantic seabirds.

ABSTRACT

We present data on digestive efficiencies and gut retention times of eight North Atlantic seabird species, fed on two fish species - Lesser Sandeel (*Ammodytes marinus*) and Whiting (*Merlangius merlangus*) - which commonly occur in the diet of wild seabirds. In an inter-specific comparison, there was a positive relationship between retention time and digestive efficiency, which we suggest represents a trade-off between conflicting benefits of efficient digestion and rapid digestion. Analysis of excretion curves revealed that retention time of digesta in the stomach was more important than passage time of digesta through the intestine in determining whole gut retention time. Differences in stomach retention time of Lesser Sandeel and Whiting explained the longer overall retention time of the latter diet. Stomach retention time and whole gut retention time was greater in species with relatively large stomachs, while intestine passage time was correlated with relative intestine length. Species which typically eat a wide range of food types, including low quality items, tended to have slow and efficient digestion and heavy stomachs, whereas species which specialise on readily digestible and energy dense food types had the opposite digestion strategy.

INTRODUCTION

Meat and fish diets are similar in nutrient balance to consumer tissues, and are relatively easy to digest (Kirkwood 1985). Recent reviews have suggested that there is rather little variation in gut retention time and digestive efficiency among the piscivorous and carnivorous bird guilds (Castro et al. 1989; Karasov 1990). One might assume, therefore, that feeding strategies of meat and fish eaters are dictated solely by considerations of prey availability. However, Barton and Houston (1993a, 1993b, 1994) showed that, in captive trials, there is considerable variation among raptor species in digestive efficiency, even when birds are fed on the same quantities of the same diet. They identified a positive relationship among species between retention time of digesta in the gut, and digestive efficiency: species which digest their food slowly seem to have higher digestive efficiency. Such a relationship is expected to occur within an individual, because the longer the food is exposed to digestive and absorptive processes in the gut, the greater the proportion of the available energy that will be assimilated (Sibly 1981; Karasov 1996).

Furthermore, Barton and Houston (1993a, 1993b, 1994) showed that the different digestion strategies (i.e. combinations of retention time and digestive efficiency, (Sibly 1981)) adopted by raptor species were related to both their gut morphology and their foraging method. Species with short retention times and low digestive efficiency had short small intestines, and tended to be active pursuers of fast-moving (mainly avian) prey. Conversely, species with long retention times and high digestive efficiency tended to have long small intestines, and to be mainly scavengers or feeders on slow moving prey. They suggested that “pursuers”, whose prey capture rate is dependent on flight performance, have evolved small guts and rapid digestion because the reduced digestive efficiency is more than compensated for by increased prey capture rates achieved through having lower body mass.

Digestion parameters of northern hemisphere seabirds are almost completely unknown. Here we report on a study of digestive efficiency and gut retention time in eight common and widespread North Atlantic seabird species, fed on two fish species which are important as prey in the wild - Lesser Sandeel (*Ammodytes marinus*) and Whiting (*Merlangius merlangus*).

Diets differ in their ease of digestion and their energy content. Some seabird species, such as Common Guillemots (*Uria aalge*), specialise on eating fish, which are easily broken down (Jackson et al. 1987), and which have high energy density (Hislop et al. 1991). Other seabirds, such as Herring Gulls (*Larus argentatus*), eat a more varied diet, including invertebrate prey which are resistant to digestion, for example shellfish and shore crabs (*Carcinus* spp.), or are low in energy density, such as earthworms (*Lumbricus* spp) (Cramp and Simmons 1977, 1983; Cramp 1985). One might predict that species in the latter group would have long retention times and large guts in order to extract sufficient nutrient from varied and low quality food (Karasov 1990), whereas species in the former group would have more rapid digestion and smaller guts, in order to benefit from the mass minimisation that such a strategy would bring about (Sibly 1981).

We examine a guild of fish eating birds, and test for an inter-specific relationship between retention time of digesta and digestive efficiency. We then investigate correlations between gross gut morphology and digestion strategy. The retention time of digesta in the two main gut compartments of seabirds - the stomach and the small intestine - can be estimated using reactor theory models of digestion (Penry and Jumars 1987). We examine the excretion curves of our study species, in order to estimate these parameters, and thereby determine whether the gastric or the intestinal component of the digestion process is the most important in determining overall gut retention time. Finally we test the hypothesis that short retention times and low digestive efficiency will be found in species which eat a narrow range of mainly high quality food items, and that long retention times and high digestive efficiency will be the strategy of species with a more catholic diet, including low quality food types.

METHODS

Digestion trial protocol

Digestion parameters of eight North Atlantic seabird species (Northern Fulmar (*Fulmarus glacialis*), Shag (*Phalacrocorax aristotelis*), Herring Gull, Great Skua (*Catharacta skua*), Black-legged Kittiwake (*Rissa tridactyla*), Common Guillemot, Razorbill (*Alca torda*), and Atlantic Puffin (*Fratercula arctica*)) were measured in Foula, Shetland (60°08'N 02°05'W), during May - July 1995. Non-breeding adults were captured and placed in individual 60 cm square polythene-lined cages, supported above plastic excreta-collecting trays, in a room with ambient temperature and natural lighting. Birds were fasted for 12 - 20 hours, until digestion of any meal eaten prior to capture was complete (indicated by the appearance of bile-like excreta). They were then fed a single meal by hand at 0900 - 1000 hours. Meal sizes were calculated to meet maintenance energy requirements over a 24 hour period following the meal (Kirkwood 1981). Meal fresh mass averaged 10.88 ± 0.28 % and 10.82 ± 0.14 % of body mass, for Whiting and Lesser Sandeel meals respectively (range 7.94 to 12.90 %). Mean daily mass loss of the birds was 1.21 ± 0.33 % (range - 5.2 to + 6.3%). Excreta collections from each bird were made at 1, 3, 5, 7, 9 and 12 hours after the meal, and then the following morning at 19, 21, 23, etc. hours after the meal, until excretion was complete (again indicated by bile-like excreta). Following the trials, birds were released at sea.

Captivity may alter digestion parameters. In rapid trials such as these, when the birds are not acclimated to captivity, digestion might be affected by stress. However, if birds are kept in captivity for considerable periods in order to acclimate them, metabolic and organ size changes may occur, which are also likely to make measured digestion parameters differ from values of wild birds (Piersma et al. 1993; Piersma et al. 1996). In this study all birds were treated identically, and thus inter-specific and inter-diet comparisons should be valid. We attempted to minimise stress by keeping the birds in a quiet building, and by minimising their exposure to humans.

Experimental diets

Lesser Sandeel of length 100 - 125 mm (equivalent to 3.2 - 6.2 g fresh mass), were obtained from Shetland waters in May 1995. Whiting of length 100 - 150 mm (mean fresh mass 21.2 ± 0.19 g), were obtained from the Irish Sea in April 1995. We selected the diets because they are abundant in the diet of most seabird species in the north-east Atlantic (Cramp and Simmons 1977, 1983; Cramp 1985). It was also anticipated that the Lesser Sandeel would have considerably higher energy density than Whiting (Hislop et al. 1991), thus providing a contrast between high quality and low quality fish diets; however, the Lesser Sandeel were in fact no more energy dense than Whiting, probably because the individuals used were obtained slightly too early in the season (see Hislop et al. 1991). However, there was a large difference between the diets in their ease of digestion (see below). Fish were double wrapped and stored at -20°C until used in feeding trials. They were thawed and fed moistened at $5-10^{\circ}\text{C}$. To determine the energy and Nitrogen content of the diets, individual Whiting and groups of three Lesser Sandeel were dried to constant mass at 55°C in a fan-assisted oven, and homogenised in a SPEX 6700 liquid Nitrogen freezer mill. Energy (kJ g^{-1} dry mass) and Nitrogen (% dry mass) content of the dried samples were determined in a Parr Adiabatic Bomb Calorimeter and a LECO FP-328 Elemental Nitrogen Analyser respectively. Water, lipid and ash content were also determined for these samples. Lipid content was determined using a Soxhlet apparatus with chloroform as solvent. Ash content was determined by combusting the dried lipid-free samples at 660°C for 12 hours in a muffle furnace. The two diets were very similar in nutrient composition and energy density (Table 2.1). We also performed an *in vitro* digestibility assay, to compare the rate at which the two fish types are broken down in acid proteolytic conditions similar to the stomach of seabirds. Lesser Sandeel samples were broken down at a much greater rate than the same mass of Whiting (Hilton et al. submitted ms a).

Determination of retention time and digestive efficiency

Excreta were scraped from the collecting trays into plastic vials, and immediately frozen at -20°C . The excreta samples were dried at 55°C in a fan-assisted oven, and dry mass of each sample was determined (± 0.001 g). For each bird, all the excreta

samples were combined, homogenised in an electric grinder, and energy and Nitrogen content were determined as for the fish samples.

Following Jackson (1992), a gravimetric method was used to determine mean retention time of digesta, which was calculated as:

$$t = \frac{\sum_{i=1}^n m_i \cdot t_i}{\sum_{i=1}^n m_i}$$

where m_i is the amount of excreta produced in the i th time interval (g dry mass), and t_i is the time (hours) since the trial meal (Blaxter et al. 1956).

Mean retention time was calculated for a 19 hour time interval (i.e. up to 0500 hours on the morning after the meal). Most birds completed digestion of the meal at around this time. A small number of birds continued to produce excreta after 19 hours, notably Northern Fulmars.

Nitrogen-corrected True Metabolisable Energy Coefficient (TMEC_N) was used as the measure of digestive efficiency (see Miller and Reinecke 1984 for explanation of the different measures which can be used). Nitrogen-corrected endogenous energy loss (EEL_N) was estimated from measurements made on Common Guillemots (n=10) and Lesser Black-backed Gulls (*Larus fuscus*) (n=6) in 1996 and 1997, using methods similar to those described by Guglielmo and Karasov (1993). Birds were maintained in the same conditions as described for the main experiment, with the exception that they were fed two meals of varying mass per day. The Common Guillemots were fed on Sprats (*Sprattus sprattus*), and the Lesser Black-backed Gulls were fed on Whiting. Linear regression of energy excreted (kJ per kg body mass) on energy ingested (kJ) was calculated for each bird-day (each bird was used on two or three consecutive days, at different intake levels). Daily energy ingested varied between 368 and 1815 kJ. There was no significant difference between the two species in the slope or the intercept of the regression line (ANCOVA, $F_{1,39} = 1.95$, n.s. and $F_{1,40} = 2.66$, n.s. for slope and intercept respectively). Therefore in estimating mass specific EEL_N per day for the species in this study we used the intercept of the common linear regression

$$y = 0.268 x + 47.5; F_{1,41} = 210, p < 0.0001, r^2 = 0.83.$$

Thus we estimated EEL_N as $47.5 \text{ kJ kg}^{-1} \text{ day}^{-1}$.

$TMEC_N$ was calculated as:

$$\frac{(Q_i \cdot GE_i) - (Q_o \cdot GE_o - EEL_N) + N_c}{Q_i \cdot GE_i}$$

where Q_i is the dry mass of food eaten and Q_o is the dry mass of excreta (g); GE_i is the energy density of the food, and GE_o is the energy density of excreta (kJ g^{-1} dry mass); N_c is a Nitrogen Correction Factor, standardising the birds to zero Nitrogen retention:

$$N_c = ((Q_i \cdot N_i) - (Q_o \cdot N_o)) \cdot 34.4 \text{ kJ g}^{-1}$$

where N_i is percent Nitrogen content of food, N_o is percent Nitrogen content of excreta, and 34.4 kJ g^{-1} is estimated energy density of excretory Nitrogen (Harris 1966).

We express $TMEC_N$ as a percentage, and for convenience refer to it hereafter as digestive efficiency. In all parametric statistical analyses we used the arcsine transformed values of digestive efficiency.

Table 2.1: Energy density and chemical composition of the two trial diets.

	Energy density (kJ g^{-1})	Protein (%)	Water (%)	Lipid (%)	Ash (%)
Lesser Sandeel	4.63	15.71	78.45	2.95	3.60
Whiting	4.41	16.09	77.47	1.89	3.42

All values expressed on a wet mass basis. Values shown are estimates for fish of the mean size used in feeding trials (4.7 g for Lesser Sandeel, 21.2 g for Whiting), calculated from power regressions of energy or component content on wet body mass.

Excretion curves of seabird species

The gut of seabirds is relatively simple, consisting of the oesophagus, a simple acid-proteolytic stomach (proventriculus and gizzard), a tubular small intestine and a very short colon. Thus, using reactor theory one can predict that the gut will function as a continuous stirred tank reactor (CSTR) - the stomach, in series with a plug-flow reactor (PFR) - the intestine (Penry and Jumars 1987). If this is the case, the cumulative output of excreta from a meal should be a negative exponential function, with the x-intercept offset from time zero. The x-intercept of the fitted excretion curve is transit time - the time between meal ingestion and first excreta production - and estimates passage time of digesta through the PFR (intestine). The inverse of the slope of a plot of log excretion rate against time since feeding estimates mean retention time of digesta in the CSTR (stomach). Following Karasov and Cork (1996), we fitted a negative exponential function to the cumulative excretion curve of each seabird species on each diet:

$$\% \text{ meal mass excreted} = \Phi(1 - \exp(-b(t - t_t)))$$

where Φ is asymptotic mass of excreta produced, t is time since feeding, and t_t is transit time. In all cases a very good fit to the data was found, (adjusted r^2 of non-linear regressions ≥ 0.99), and we therefore estimated passage time through the intestine as the x-intercept of the fitted curve. To calculate mean retention time of digesta in the stomach we plotted log excretion rate against time since feeding for each individual bird, and estimated stomach retention time as the inverse of the slope of the plot.

Gut morphology measurements

We measured the small intestine length and the stomach mass of the study species by dissection of victims of scientific culls, collisions, or pest control. All dissected birds were adults which died during May - July; we discarded birds which were malnourished, dehydrated or not frozen rapidly after death. Birds were stored double-wrapped at -20°C , and thawed for 10 - 20 hours at $5 - 10^\circ\text{C}$ prior to dissection. We excised the entire gut from the cloaca to the syrinx. The small intestine was isolated, and, using a blunt scalpel, sufficient mesentery and fat were carefully removed to allow it to be straightened. The tissue was allowed to relax in avian

ringer solution (Hale 1965) for 15 minutes prior to measurement, and was then placed on a smooth surface, which was wetted with avian ringer. It was straightened, but not pulled out under tension, and the length measured (± 1 mm) from the pyloric junction to the ileo-caecal junction. The empty stomach was dried to constant mass at 55°C in a fan-assisted oven, and weighed (± 0.001 g).

In analysis of the relationship between gut morphology and digestion parameters, we used standardised residual digestive organ sizes, calculated from linear regressions using \log_{10} -transformed body mass and organ size variables. No correction for body mass was made in analysis of digestion parameters, because there was no evidence for a relationship between body mass and mean retention time or digestive efficiency among our study species (linear regression of log mean retention time on log body mass: $F_{1,6} = 0.09$, $p = 0.78$; linear regression of log digestive efficiency on log body mass, $F_{1,6} = 0.29$, $p = 0.61$). Means are presented ± 1 s.e.m..

RESULTS

Digestion parameters and the digestive efficiency - retention time trade-off

Mean digestive efficiencies of the study species fell within the range 75.81 - 83.30% on both diets (Table 2.2). Two-way ANOVA indicated that digestive efficiency did not differ between diets (diet effect, $F_{1,73} = 2.03$, n.s.), and there was no significant species - diet interaction ($F_{7,66} = 1.81$, n.s.). However there were significant differences between seabird species in digestive efficiency (species effect, $F_{7,74} = 13.4$, $p < 0.001$). Post-hoc tests (Student-Newman-Keul) indicate that Black-legged Kittiwake had significantly lower digestive efficiency than all other species, and that Northern Fulmar had significantly higher digestive efficiency than all other species. Great Skua had a higher digestive efficiency than the three auk species, (as well as Black-legged Kittiwake).

Table 2.2: Digestion parameters of the study species on the two trial diets.

Species	Sandeel		Whiting	
	Digestive efficiency (%)	Retention time (hours)	Digestive efficiency (%)	Retention time (hours)
Shag	80.99±0.51	6.61±0.28	79.52±0.52	7.31±0.48
Northern Fulmar	82.65±0.47	9.65±0.72	83.94±0.57	10.80±0.58
Great Skua	80.35±0.52	6.83±0.	82.80±1.26	8.24±0.33
Black-legged Kittiwake	74.46±0.56	6.43±0.17	77.16±0.37	7.02±0.50
Herring Gull	80.23±0.99	7.05±0.17	79.40±0.51	7.22±0.28
Common Guillemot	77.52±0.92	5.83±0.14	79.25±1.35	6.81±0.24
Razorbill	78.97±0.77	5.84±0.14	77.54±1.75	7.40±0.50
Atlantic Puffin	77.96±0.62	6.29±0.28	78.58±0.94	7.11±0.29

Values are means ± s.e.m.. n = 5 for each species - diet group, except for Northern Fulmar (n = 6 in both diet groups), Atlantic Puffin (n = 6 in Whiting group) and Common Guillemot (n = 6 in Whiting group). Digestive efficiency is Nitrogen-corrected True Metabolisable Energy Coefficient, expressed as a percentage. Retention time is mean 19-hour gut retention time, calculated by a gravimetric method.

Northern Fulmar had the longest retention time, by a large margin (Table 2.2). Mean retention time of the other seven species lay between 6.32 hours for Common Guillemot, and 7.53 hours for Great Skua. In two-way ANOVA, there was a significant effect of both diet and species on mean retention time (diet effect $F_{1,73} = 13.1$, $p=0.001$; species effect $F_{7,73} = 20.8$, $p<0.001$), but no significant species - diet interaction ($F_{7,66} = 0.97$, n.s.). Retention times were longer on the Whiting diet than on the Sandeel diet.

In an inter-specific comparison, digestive efficiency was positively related to gut retention time ($r_s = 0.76$, $n = 8$, $p = 0.028$) (Fig 2.1).

Excretion curves of seabird species

Figure 2.2 illustrates typical cumulative excreta production curves for the study species, showing the offset negative exponential curve, reaching an asymptote at around 19 hours after feeding. Analysis of the excretion curves showed that, in all cases, estimated retention time of digesta in the stomach greatly exceeds the estimated time taken for passage through the small intestine (Table 2.3), and thus the former might therefore be expected to be the main determinant of overall gut retention time. To test this we used stomach retention time and intestine passage time as covariates in an ANOVA with gut retention time as dependent variable. This showed for Sandeel:

Log_{10} mean retention time = $0.39 \times \text{log}_{10}$ stomach retention time + $0.18 \times \text{log}_{10}$ intestine passage time. $F_{2,5} = 24.3$, $p = 0.003$, $r^2 = 0.91$.

Partial effects: stomach retention time $t = 6.39$, $p = 0.01$; intestine passage time $t = 1.20$, n.s.,

and for Whiting:

Log_{10} mean retention time = $0.38 \times \text{log}_{10}$ stomach retention time + $0.05 \times \text{log}_{10}$ intestine passage time. $F_{2,5} = 13.6$, $p = 0.01$; $r^2 = 0.84$.

Partial effects: stomach retention time $t = 5.07$, $p = 0.004$; intestine passage time $t = 1.10$, n.s..

Stomach retention time was therefore a very good predictor of total gut retention time, but intestine passage time was not.

Taking mean values for each species on each diet, stomach retention time of Whiting was significantly greater than Lesser Sandeel (Wilcoxon Matched-pairs, $z = 2.38$, $p = 0.017$); however passage time of digesta through the small intestine did not differ between diets (Wilcoxon Matched-pairs, $z = 0.28$, n.s.).

Table 2.3: Estimates of intestine passage time and stomach retention time of digesta, based on excretion curves.

Species	Intestine Passage Time (mins \pm s.e.)		Stomach Retention Time (mins \pm s.e.m.)	
	Sandeel	Whiting	Sandeel	Whiting
Shag	73.5 \pm 8.0	56.8 \pm 5.9	171 \pm 11.2	258 \pm 37.4
Northern Fulmar	76.4 \pm 18.5	85.4 \pm 22.8	630 \pm 111	636 \pm 123
Great Skua	40.5 \pm 11.1	23.1 \pm 18.8	280 \pm 28.8	360.1 \pm 40.6
Black-legged Kittiwake	37.6 \pm 2.9	48.4 \pm 9.2	261 \pm 14.4	291 \pm 44.7
Herring Gull	61.4 \pm 3.5	49.4 \pm 1.6	239 \pm 23.5	284 \pm 20.4
Common Guillemot	69.0 \pm 6.2	32.5 \pm 7.5	164 \pm 23.6	324 \pm 21.4
Razorbill	49.7 \pm 5.5	68.5 \pm 11.2	221 \pm 13.3	300 \pm 51.4
Atlantic Puffin	71.3 \pm 2.5	92.7 \pm 3.2	229 \pm 21.3	227 \pm 12.7

Intestine passage time was estimated as the x-intercept of a negative exponential curve fitted to cumulative excretion plots for each species - diet combination. Stomach retention time estimated as reciprocals of slopes of semi-log plots of excretion rate on time since feeding, calculated for each individual bird.

Fig 2.1: The relationship between digestive efficiency and digestion rate in seabird species.

Open circles: generalist feeding species; closed circles: specialist piscivores.

Digestive efficiency is Nitrogen-corrected True Metabolisable Energy Coefficient, expressed as a percentage. Retention time is mean 19-hour gut retention time, calculated by a gravimetric method. Values shown are averages for the two trial diets \pm s.e.m..

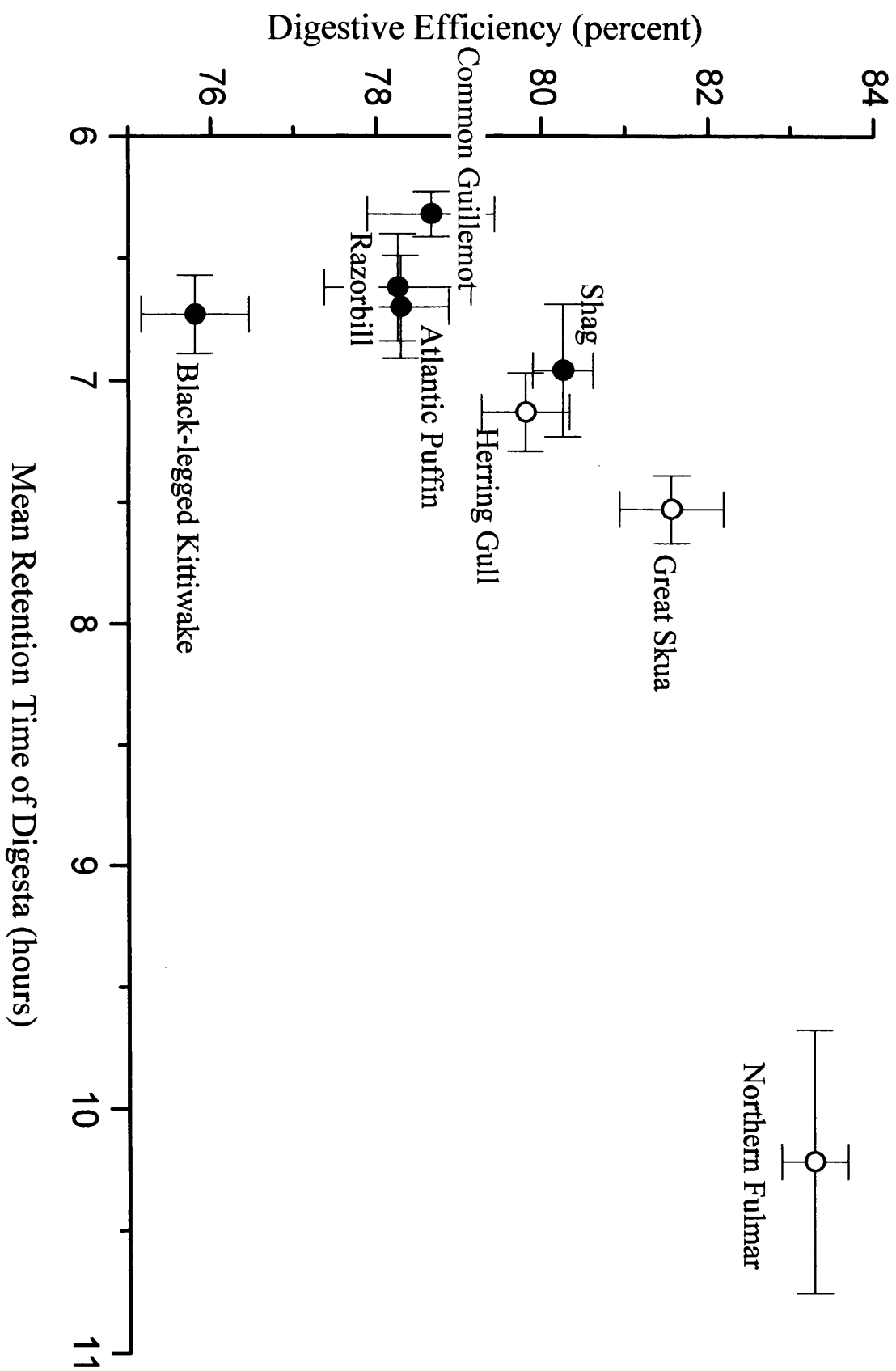
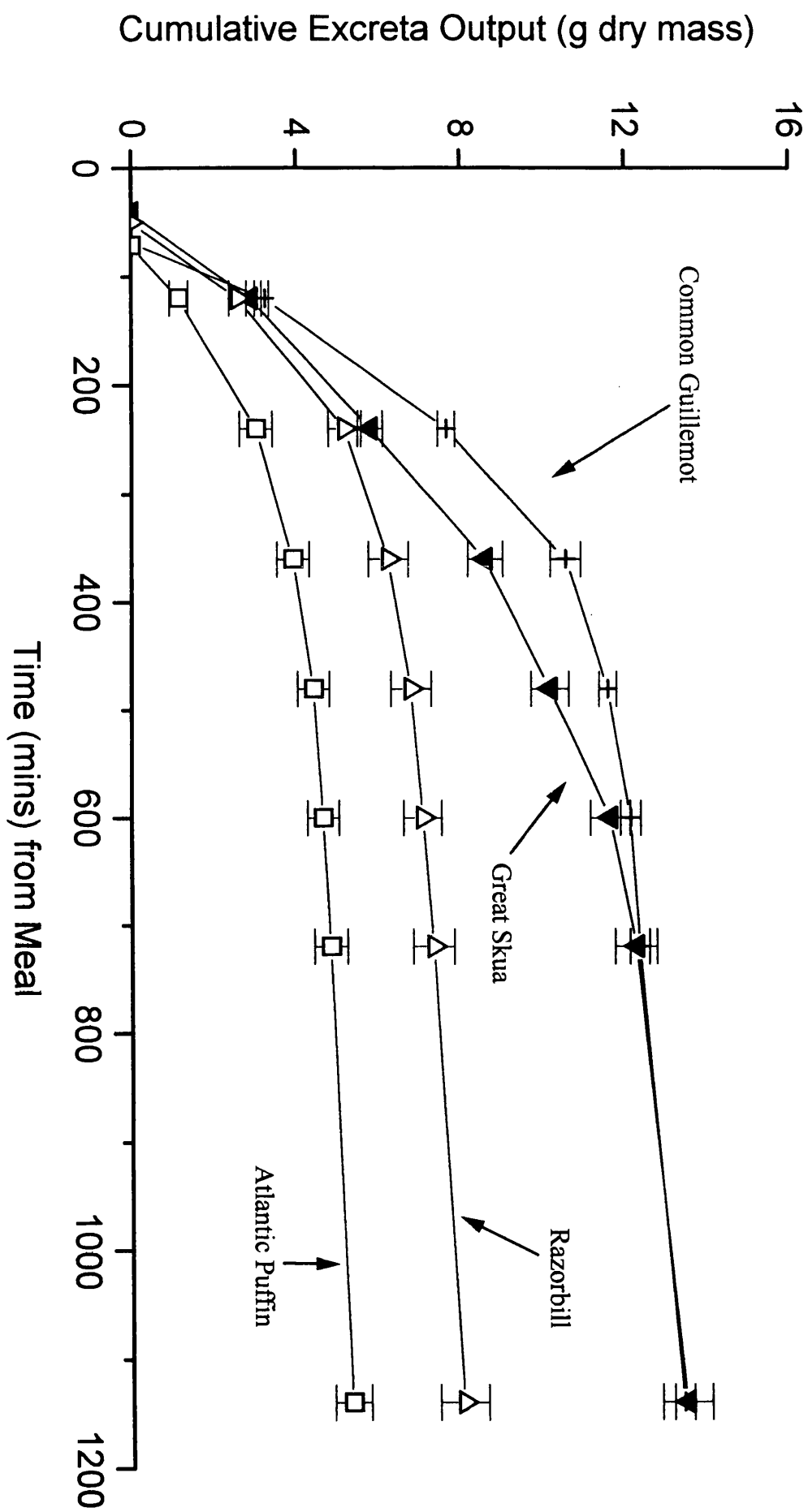


Fig 2.2: Cumulative excreta production curves for four of the study species, on a Sandeel diet.



Relationship between digestion parameters and gross gut morphology

In the absence of any species - diet interactions in the foregoing analyses of gut retention time and digestive efficiency, we used the seabird species' overall mean values of retention time and digestive efficiency in examining the relationship between digestion parameters and gut morphology.

For seabird species, residual small intestine length was not correlated with mean retention time of digesta ($r_s = 0.14$, $n = 8$, n.s.). There was, however, a relationship between residual stomach mass and retention time ($r_s = 0.69$, $n = 8$, $p = 0.058$). Northern Fulmar and Shag have rather different gross gut morphology to the six Charadriiform species which make up the remainder of the analysis, reflecting their separate phylogenetic origins. Repeating the analysis for the six Charadriiform species alone shows the same relationship between stomach mass and retention time ($r_s = 0.83$, $n = 6$, $p = 0.040$).

Estimated passage time of digesta through the small intestine was positively correlated with residual small intestine length ($r_s = 0.74$, $n = 8$, $p = 0.037$), and estimated retention time of digesta in the stomach was positively correlated with residual stomach mass ($r_s = 0.76$, $n = 8$, $p = 0.028$).

Digestion parameters and the feeding ecology of seabirds

We divided our study species into dietary generalists and dietary specialists, based on published information on typical breeding season diets (Cramp and Simmons 1977, 1983; Bradstreet and Brown 1985; Cramp 1985; Furness and Barrett 1991). We classified Northern Fulmar, Great Skua and Herring Gull as generalists, which take a varied diet, including significant proportions of non-fish food items, some of which are resistant to digestion and/or of low energy density. Shag, Black-legged Kittiwake, Common Guillemot, Razorbill and Atlantic Puffin were classified as specialists, which eat mainly small, readily digestible fish of high energy density.

Digestive efficiency was greater and retention time was longer in generalist species than in specialist species (Mann-Whitney U-Test, $p = 0.053$ and 0.025 respectively) (Fig 2.1). Furthermore, residual stomach mass was also greater in generalists than specialists (Mann-Whitney U-Test, $p = 0.025$), but residual intestine length did not

differ between specialists and generalists (Mann-Whitney U-Test, $p > 0.10$) (Fig 2.3a, 2.3b).

Figure 2.3a: Dry mass of stomach as a function of body mass in the study species.

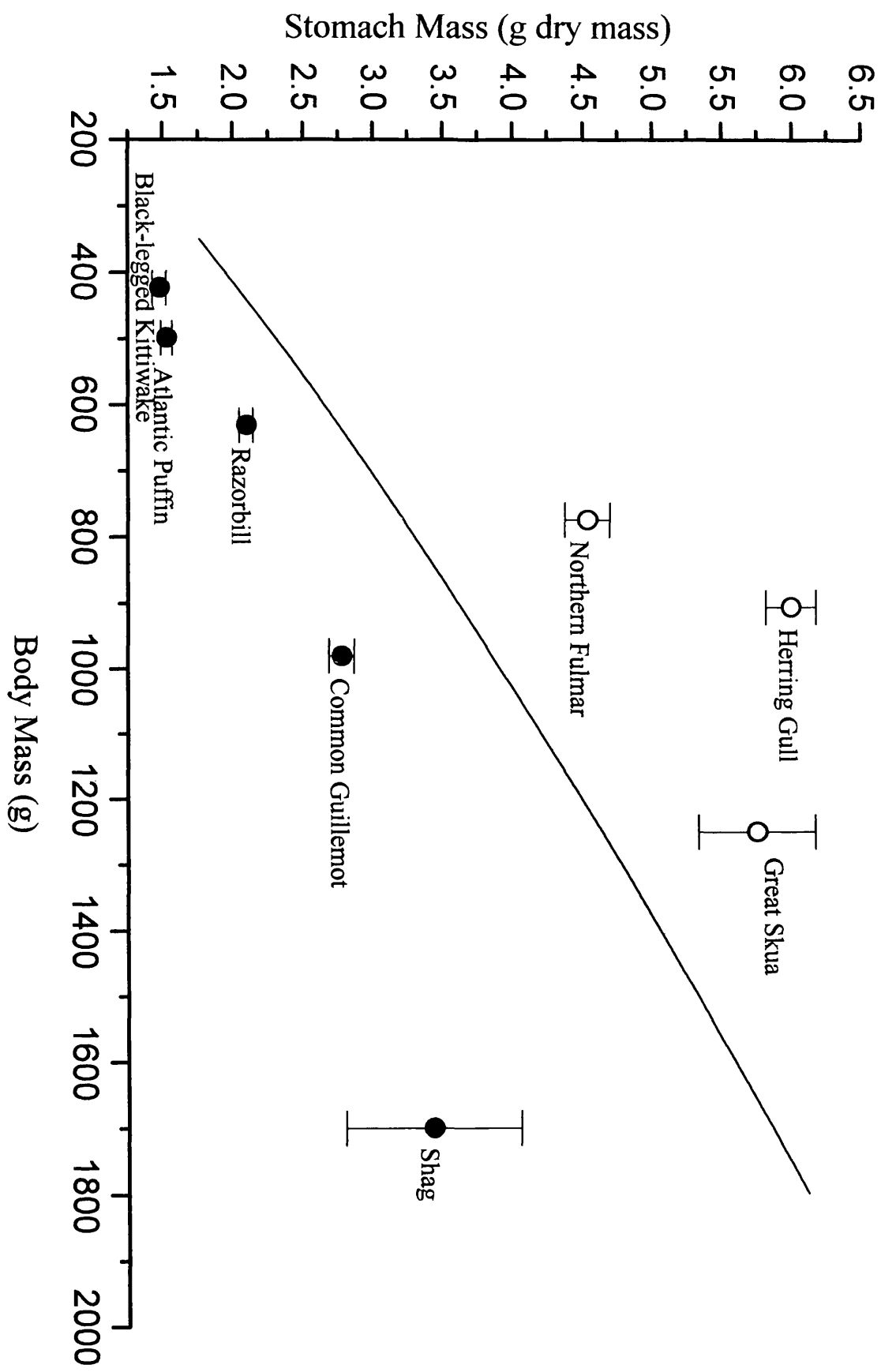
Figure 2.3b: Small intestine length as a function of body mass in the study species.

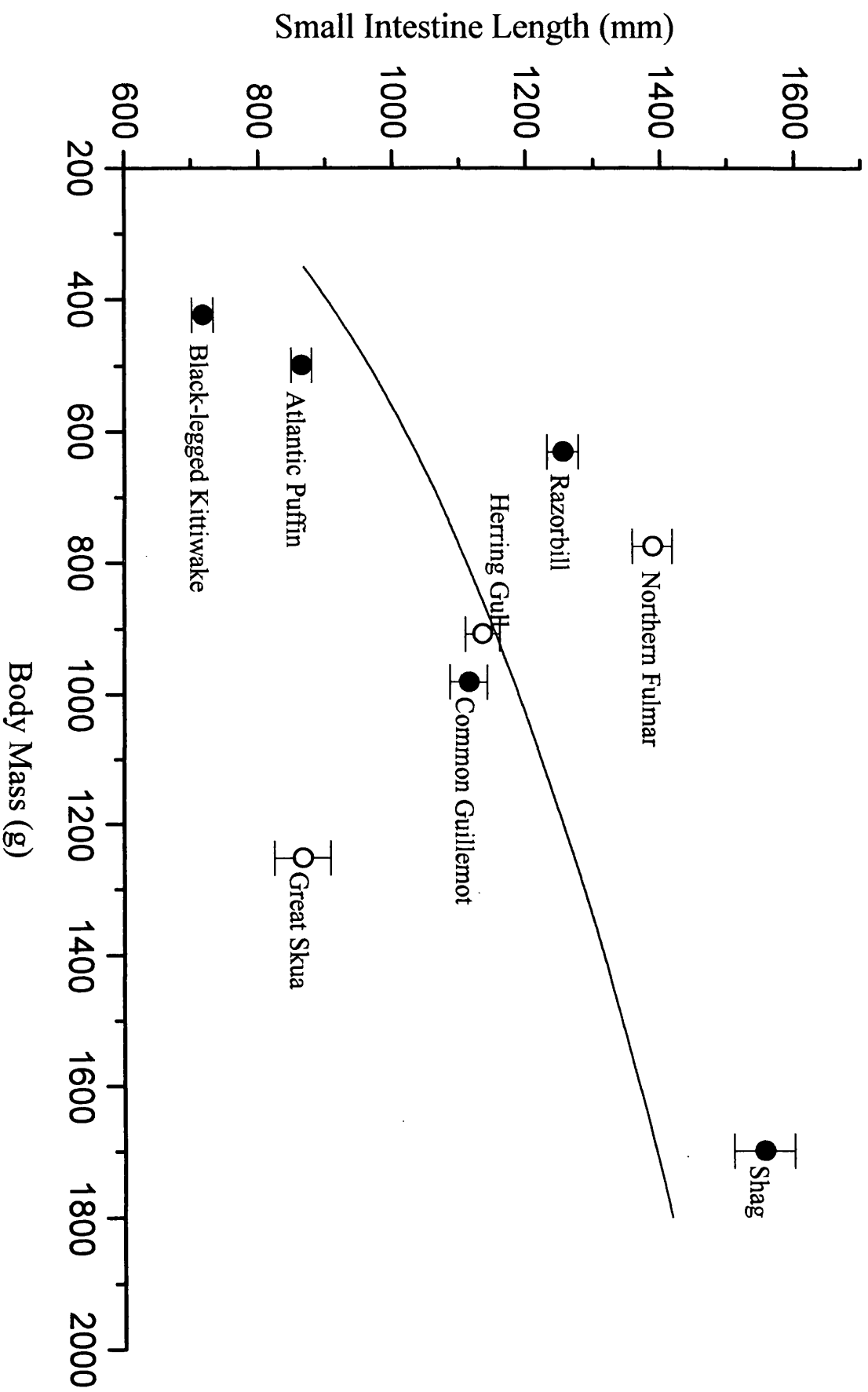
Open circles: generalist feeding species; closed circles: specialist piscivores.

Values are means \pm s.e.m.. Body mass is the mean value for the dissected birds.

Shag n=10; Northern Fulmar n=23; Great Skua n=7; Black-legged Kittiwake n =21;

Herring Gull n=28; Common Guillemot n=22; Razorbill n=20; Atlantic Puffin n=20.





DISCUSSION

Digestive efficiency - retention time trade-off

We have shown that, as for raptor species (Barton and Houston 1993b), there is variation in digestion parameters between seabird species, and an apparent trade-off between digestion rate (the inverse of retention time) and digestive efficiency. The Black-legged Kittiwake and the three auk species seem to be rather rapid digesters, paying a cost of slightly lower digestive efficiency compared to the other species. This means that they must capture more prey each day in order to gain the same amount of metabolisable energy.

Morphological correlates of retention time

In raptors, short retention times are achieved mainly by reducing the length of the small intestine (Barton and Houston 1993a). However, among seabirds, whilst there was a correlation between small intestine length and passage time of digesta through the intestine, there was no relationship between small intestine length and whole gut retention time. Stomach mass, which was correlated with stomach retention time, was a far more important influence on whole gut retention time. Separate estimates of retention time of digesta in the stomach and passage time through the intestine provide an explanation: the former greatly exceeds the latter, and therefore between-species variation in intestine passage time has little effect on overall gut retention times.

We can conclude therefore that digesta were retained in the stomach for longer in species with relatively heavy stomachs, and that this resulted in an overall correlation between relative stomach mass and gut retention time. Passage of digesta through the intestine was faster in species with relatively short small intestines, but this has only a small (and non-significant) effect on overall gut retention times.

Because acid-proteolytic breakdown of Whiting *in vitro* was slower than Lesser Sandeel (Hilton et al. submitted ms a), one would predict that *in vivo* gastric retention time of Whiting would be greater than that of Lesser Sandeel. There was however very little difference between the diets in energy density or nutrient composition (or in the amount eaten). Therefore one might also predict that, once broken down in the stomach, the time taken for digestion and absorption processes in the small intestine

should not differ between diets. The data from excretion curves support these predictions. The between-diet difference in whole gut retention times arose because Whiting was retained for longer in the stomach than Lesser Sandeel; there was no difference between diets in intestine passage rates.

Digestion strategies and feeding ecology of seabirds

We have shown a link between digestion strategy of seabirds and their diet. Species with a catholic diet, including low quality food items, tend to have a strategy of slow and efficient digestion. Species which specialise on fish, which are relatively easy to digest (Jackson et al. 1987) and are energy dense (Hislop et al. 1991), tend to have short retention times. We suggest that dietary generalists are adapted for the successful digestion of poorly digestible foods, which require long retention times. When fed on the same diet, slow digesting generalists thus achieve a higher digestive efficiency than specialists, by virtue of their longer retention times. A similar association between the digestibility of the diet, gut retention time, and digestive efficiency was found in a comparison of two land crab species (Greenway and Raghaven 1998).

It has been suggested that short retention times are beneficial, despite the reduction in digestive efficiency, because rapid production of excreta from a meal produces mass savings (Sibly 1981). It was proposed that short intestines and rapid digestion are adaptive for pursuit foraging raptors, because their hunting success is strongly mass-dependent. For searching foragers, which find slow moving prey or carrion, there is no such advantage (Barton and Houston 1993a, 1993b, 1994). For seabirds the pursuer - searcher dichotomy is still apparent: the specialist piscivores - with the exception of Black-legged Kittiwake - are also pursuit foragers, whereas the generalist feeders are searchers and scavengers. However, prey capture method is unlikely to be the only factor explaining how digestion strategies vary among seabird species. In a recently developed model (Hilton et al. submitted ms b) we have shown that rapid digestion can produce time and energy savings for seabirds through reducing the effect of an "ingestion bottleneck": because they feed relatively infrequently, at foraging sites well removed from the nest sites, seabirds in the breeding season have to eat large meals on each feeding trip. If on a given feeding

trip the gut becomes full of food, the bird is constrained to eat only at the rate at which it can make space in the gut by excretion. Rapid digestion minimises the impact of this bottleneck, but has the cost of reducing digestive efficiency. Model outcomes suggested that avoidance of the ingestion bottleneck is more important in species for which flight to and from feeding sites is expensive in time and energy, whilst high digestive efficiency is more advantageous for species with low flight costs. Among the “specialists”, the auks and Shag have relatively high power output in flight, due to high wing loadings, although the Black-legged Kittiwake does not. By contrast, the generalist species have less energetically expensive flight, due to their lower wing loadings and frequent use of soaring and gliding flight (Pennycuick 1987). Furthermore the auks and Black-legged Kittiwake tend to forage further offshore than Herring Gull and Great Skua (Cramp and Simmons 1983; Cramp 1985; Phillips et al. in press). Northern Fulmars are a different case. Instead of the short commuting trips between nesting site and feeding site made by the other species, they make very prolonged and wide-ranging foraging trips, in which several meals are probably consumed (Cramp and Simmons 1977).

Generalist feeders have significantly heavier stomachs than specialists, presumably because of the greater effort required to break down such prey items as shellfish and hard bodied arthropods. A relationship between stomach mass and the ease with which the diet is broken down has been shown among duck species, waders and lorikeets (Kehoe and Ankney 1985; Kehoe and Thomas 1987; Richardson and Wooller 1990; Piersma et al. 1993). Another factor might be that species eating energy dilute food have to eat large amounts in order to meet energy requirements, and therefore need large stomachs (Miller 1975). Specialist feeders may benefit from having small, light stomachs because of the high metabolic cost of maintaining gut tissue (Schmidt-Nielsen 1990). The mass savings which are made may also reduce energy costs of flight (Pennycuick 1989), and improve prey-capture rates. Reductions in stomach size prior to migration, apparently as an energy saving mass-reduction tactic, have been noted in wading birds (Piersma 1998). It might be expected that, if fed the same (readily digestible) diet, species with heavier stomachs would be able to process food faster than species with light stomachs, because their

gastric musculature would be more powerful (Piersma et al. 1993). However, this is evidently not the case among our study species.

We have shown that species which specialise on readily digestible, energy dense fish prey tend to have a rapid and inefficient digestion strategy. The small stomachs and inefficient digestion of these specialist feeders may restrict their ability to process relatively less digestible foods, and constrain them to select only energy dense prey types which can be readily digested. Such an effect has been shown intraspecifically in waders (Piersma et al. 1993). Indeed, captive Common Guillemots fed *ad libitum* on Norway Pout (*Trisopterus esmarki*), which has very low energy density, were unable to maintain body mass (H. Brugge *pers comm.*).

Thus one can interpret the relationships between digestion strategy, gut morphology and feeding ecology described in this study as representing a suite of co-evolved characteristics. Specialising on high quality digestible food is associated with rapid digestion and reduction in stomach mass, whereas eating low quality foods is associated with slow but efficient digestion and well developed stomachs.

Further investigation of these relationships would be desirable, because there are some problems of common phylogeny in the data set (see Harvey and Pagel 1991). Most notably, the three auk species have similar feeding ecology and digestion strategies (Bradstreet and Brown 1985). These problems are unavoidable given the relatively small number of species that could be studied. It should be noted that Black-legged Kittiwake is phylogenetically closer to Herring Gull and Great Skua than it is to the auks (Sibley and Ahlquist 1990), but it shows an "auk-like" digestion strategy of short retention time, and small stomach, which would be expected from its generally high quality diet (Cramp and Simmons 1983).

Digestive efficiency of North Atlantic seabird species

The only previous measures of digestive efficiency in northern hemisphere seabird species were reported for Black-legged Kittiwake and Brünnich's Guillemot (*Uria lomvia*), fed on Capelin (*Mallotus villosus*) and Arctic Cod (*Boreogadus saida*), and are slightly lower than those reported here (Brekke and Gabrielsen 1994). Our measures of endogenous energy losses in seabirds are higher than those reported for other bird species (Guglielmo and Karasov 1993), possibly reflecting the rather high

metabolic rates of seabirds (Ellis 1984), which might result in high rates of tissue turnover. Since accounting for endogenous energy losses in excreta increases the estimate of digestive efficiency, these high values possibly explain why the True Metabolisable Energy Coefficient values reported here tend to be slightly higher than most published values of Apparent Metabolisable Energy Coefficient in other piscivores (Castro et al. 1989; Karasov 1990; Robertson and Newgrain 1992; Bennett and Hart 1993; Brugger 1993; Brekke and Gabrielsen 1994). The digestive efficiency values reported here are also somewhat higher than the 75% generally assumed in bioenergetic models of seabird fish consumption (e.g. Furness 1978; Woehler 1997); sensitivity tests have suggested that estimates of fish consumption by seabird communities are very sensitive to the value chosen for digestive efficiency (Furness 1978; Wiens 1984), hence adjusting the estimates upwards may be a useful refinement of the models.

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LITERATURE CITED

- Barton, N.W.H. and Houston, D.C. 1993a. A comparison of digestive efficiency in birds of prey. - *Ibis* 135: 363-371.
- Barton, N.W.H. and Houston, D.C. 1993b. The influence of gut morphology on digestion time in raptors. - *Comp. Biochem. Physiol.* 105A: 571-578.
- Barton, N.W.H. and Houston, D.C. 1994. Morphological adaptation of the digestive tract in relation to feeding ecology of raptors. - *J. Zool (Lond.)* 232: 133-150.
- Bennett, D.C. and Hart, L.E. 1993. Metabolizable energy of fish when fed to captive great blue herons (*Ardea herodias*). - *Can. J. Zool.* 71: 1767-1771.
- Blaxter, K.L., Graham, N.M. and Wainman, F.W. 1956. Some observations on the digestibility of food by sheep, and on related problems. - *Brit. J. Nutrition* 10: 69-91.
- Bradstreet, M.S.W. and Brown, R.G.B. 1985. Feeding ecology of the Atlantic Alcidae. - In: Nettleship, D.N. and Birkhead, T.R. (eds.) *The Atlantic Alcidae: The evolution, distribution and biology of the Auks inhabiting the Atlantic Ocean and adjacent water areas*. Academic Press, London, pp. 264-318.
- Brekke, B. and Gabrielsen, G.W. 1994. Assimilation efficiency of adult Kittiwakes and Brünnich Guillemots fed Capelin and Arctic Cod. - *Polar Biol.* 14: 279-284.
- Brugger, K.E. 1993. Digestibility of 3 fish species by Double-crested Cormorants. - *Condor* 95: 25-32.
- Castro, G., Stoyan, N. and Myers, J.P. 1989. Assimilation efficiency in birds: a function of taxon of food type ? - *Comp. Biochem. Physiol.* 92A: 271-278.
- Cramp, S. 1985. *Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic; Volume 4: Terns to Woodpeckers*. - Oxford University Press, Oxford.
- Cramp, S. and Simmons, K.E.L. 1977. *Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic; Volume 1: Ostrich to Ducks*. - Oxford University Press, Oxford.

- Cramp, S. and Simmons, K.E.L. 1983. Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic; Volume 3: Waders to Gulls. - Oxford University Press, Oxford.
- Ellis, H.I. 1984. Energetics of free-ranging seabirds. In: Rahn, H. and Whittow, G.C. (eds.) Seabird energetics. Plenum Press, New York, pp. 203-234.
- Furness, R.W. 1978. Energy requirements of seabird communities: a bioenergetics model. - J. Of Anim. Ecol. 47: 39-53.
- Furness, R.W. and Barrett, R.T. 1991. Seabirds and fish declines. - Nat. Geogr. Res. & Explor. 7, 82-95.
- Greenway, P. and Raghaven, S. 1998. Digestive strategies in two species of leaf-eating crabs (Brachyura:Gecarcinidae) in a rain forest. Physiol. Zool. 71, 36-44.
- Guglielmo, C.G. and Karasov, W.H. 1993. Endogenous mass and energy-losses in Ruffed Grouse. - Auk 110: 386-390.
- Hale, I.J. 1965. Biological laboratory data. Methuen Publishing Co., Bath, UK.
- Harris L.E. 1966. Biological energy interrelationships and glossary of energy terms. Nat Acad Sci Publ 1411, Washington D.C.
- Harvey, P.H. and Pagel, M.D. 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford.
- Hilton, G.M., Houston, D.C. and Furness, R.W. submitted a. Which components of diet quality affect retention time of digesta in seabirds? Functional Ecology.
- Hilton, G.M., Ruxton, G.D., Furness, R.W. and Houston, D.C. submitted b. Optimal digestion strategies in seabirds: a modelling approach. Evolutionary Ecology.
- Hislop, J.R.G., Harris, M.P. and Smith, J.G.M. 1991. Variation in the calorific value and total energy content of the Lesser Sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. - J. Zool. (Lond.) 224: 501-517.
- Jackson, S. 1992. Do seabird gut sizes and mean retention times reflect adaptation to diet and foraging method. - Physiol. Zool. 65: 674-697.
- Jackson, S., Duffy, D.C. and Jenkins, J.F.G. 1987. Gastric digestion in marine vertebrate predators: *in vitro* standards. - Funct. Ecol. 1: 287-291.

- Karasov, W.H. 1990. Digestion in birds: chemical and physiological determinants and ecological implications. - *Stud Avian Biol.* 13: 391-415.
- Karasov, W.H. 1996. Digestive plasticity in avian energetics and feeding ecology. - In: Carey, C. (ed.) *Avian Energetics*. Chapman and Hall, New York, pp.61-84.
- Karasov, W.H. and Cork, S.J. 1996. Test of a reactor-based digestion optimization model for nectar-eating Rainbow Lorikeets. - *Physiol. Zool.* 69: 117-138.
- Kehoe, F.P. and Ankney, C.D. 1985. Variation in digestive organ size among five species of diving ducks (*Aythya* spp.). - *Can. J. Zool.* 63: 2339-2342.
- Kehoe, F.P. and Thomas, V.G. 1987. A comparison of interspecific differences in the morphology of external and internal feeding apparatus among North American Anatidae. *Can. J. Zool.* 65, 1818-1822.
- Kirkwood, J.K. 1981. Maintenance energy requirements and rate of weight loss during starvation in birds of prey. In: Cooper, J.E. and Greenwood, A.G. (eds.) *Recent advances in the study of raptor diseases*. Chiron. Publications, Keighley, UK, pp. 153-157.
- Kirkwood, J.K. 1985. Food requirements for deposition of energy reserves in raptors. In: Newton, I. and Chancellor, R.D. (eds.) *Conservation studies on raptors: Proceedings of the ICBP World Conference on Birds of Prey, 1982*. International Council for Bird Preservation, Cambridge, UK, pp. 295-298.
- Miller, M.R. 1975. Gut morphology of Mallards in relation to diet quality. - *J. Wildl. Mgmt.* 39: 168-173.
- Miller, M.R. and Reinecke, K.J. 1984. Proper expression of metabolizable energy in avian energetics. - *Condor* 86: 396-400.
- Pennycuik, C.J. (1987) Flight of auks (Alcidae) and other northern seabirds compared with southern Procellariiformes - ornithodolite observations. *J. Exp. Biol.* 128: 335 - 347.
- Pennycuik, C.J. 1989. *Bird flight performance: A practical calculation manual*. - Oxford University Press, Oxford, UK.

- Penry, D.L. and Jumars, P.A. 1987. Modelling animal guts as chemical reactors. - Am. Nat. 129: 69-96.
- Phillips R.A., Ratcliffe, N. and Riley H.T. In Press. Factors influencing the foraging range and marine distribution of UK seabirds with an evaluation of possible marine extensions to Special Protection Areas in Scotland. Scottish Natural Heritage Research & Advisory Series, Scottish Natural Heritage, Edinburgh, UK.
- Piersma, T. 1998. Guts don't fly: small digestive organs in obese Bar-tailed Godwits. Auk 115, 196-203.
- Piersma, T., Bruinzeel, L., Drent, R., Kersten, M., Vandermeer, J. and Wiersma, P. 1996. Variability in basal metabolic-rate of a long-distance migrant shorebird (Red Knot, *Calidris canutus*) reflects shifts in organ sizes. - Physiol. Zool. 69: 191-217.
- Piersma, T., Koolhaas, A. and Dekinga, A. 1993. Interactions between stomach structure and diet choice in shorebirds. - Auk 110: 552-564.
- Richardson, K.C. and Wooller, R.D. 1990. Adaptations of the alimentary tracts of some Australian Lorikeets to a diet of pollen and nectar. Aust. J. Zool. 38, 581-586.
- Robertson, G. and Newgrain, K. 1992. Efficacy of the tritiated-water and Na-22 turnover methods in estimating food and energy-intake by Emperor Penguins *Aptenodytes forsteri*. - Physiol. Zool. 65: 933-951.
- Schmidt-Nielsen, K. 1990. Animal physiology - adaptation and behaviour. Cambridge University Press, Cambridge.
- Sibley, C.G. and Ahlquist, J.E. 1990. Phylogeny and classification of birds: A study in molecular evolution. Yale University Press, London.
- Sibly, RM 1981. Strategies of digestion and defaecation. - In: Townsend, C.R. and Calow, P.(eds.) Physiological Ecology: an evolutionary approach to resource use. Blackwell Scientific Publications, Oxford, pp. 109-139.
- Wiens, J.A. 1984. Modelling the energy requirements of seabird populations. In: Rahn, H. and Whittow, G.C. (eds.) Seabird energetics. Plenum Press, New York.
- Woehler, E.J. 1997. Seabird abundance, biomass and prey consumption within Prydz Bay, Antarctica, 1980/1981-1992/1993. Polar Biol. 17, 371-383.

chapter 3

OPTIMAL DIGESTION STRATEGIES IN SEABIRDS:

A MODELLING APPROACH

submitted for publication in *Evolutionary Ecology* as:

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ABSTRACT

Experiments show that there are marked differences between seabird species in gut retention times and digestive efficiencies, even when eating the same amounts of the same diets. We use mathematical modelling to explore the relationship between optimal avian digestion strategy and ecological factors. The key factor determining the performance of a given digestive strategy is an "ingestion bottleneck", which forces individuals to reduce their ingestion rate once the gut is full of digesta. The severity of the bottleneck is related to the retention time of digesta, with the result that an individual's optimal time and energy management differs according to digestion strategy. The model predicts that rapid (and thus inefficient) digestion is likely to be favoured when the energy cost of commuting between feeding and nesting sites is large, whereas slow (but efficient) digestion is preferable where flight energy costs are small.

INTRODUCTION

It is well known that diet type influences gut retention time, digestive efficiency and gut morphology (e.g. Warner 1981; Demment and Van Soest 1985; Karasov and Diamond 1988; Castro *et al.* 1989; Karasov 1990, 1996). However, during experiments on digestion in birds of prey (Barton and Houston 1993a; 1993b; 1994) and seabirds (Jackson 1992; Hilton *et al.* submitted ms), there was marked variation in digestion parameters among species feeding on the same diet. For birds of prey, Barton and Houston (1993a, 1993b, 1994) explained this variation in terms of differences between the study species in feeding ecology. They argued that a key feature of the digestive process was the cost of carrying ingested food, whether expressed as reduced prey capture rates, increased energy expenditure in flight, or increased predation risk. Calder *et al.* (1990) showed that male hummingbirds may keep the gut nearly empty for much of the day, even when food is abundant, apparently in order to improve flight performance. Similarly, if retention time determines the rate at which new food can be eaten, then slow digestion (i.e. long retention time) may prolong (or curtail) feeding bouts, which in turn affects time and possibly energy budgets (Kenward and Sibly 1977; Diamond *et al.* 1986; Zwarts and Dirksen 1990; Kersten and Visser 1996). It is clear that retention time (and so digestion strategy more generally) will affect an individual's fitness indirectly through the factors above. The "digestion paradigm" (Sibly 1981; Karasov 1996) predicts that the proportion of available energy that is absorbed from a meal is a function of the time that the digesta is held in the gut. This means that digestive efficiency is causally related to gut retention time, in what can be considered as a trade-off: long retention times result in high digestive efficiency, but may have indirect costs; short retention times give rise to low digestive efficiency, but may have indirect benefits.

Here we model some of these indirect effects for seabird species, and determine how aspects of fitness vary according to digestion strategy. Specifically, we develop time-energy budgets during the chick-rearing period, for two contrasting holarctic seabird species - the Common Murre, *Uria aalge*, and the Herring Gull, *Larus argentatus*. We use an experimentally derived relationship between gut retention time and digestive efficiency in these and six other seabird species (Hilton *et al.*

submitted ms) to define a set of plausible digestion strategies, and then quantify the effect of varying excretion rate on daily energy expenditure and foraging time. For each species we determine the optimal digestion strategy under a range of realistic foraging conditions. We aim to elucidate the ecological factors which are likely to lead to selection for a given digestion strategy.

We selected the two modelled species for several reasons: they are similar sized and have similar gut capacities, and yet they differ significantly in both gut retention time and digestive efficiency when given the same quantities of the same diets (G. Hilton unpubl. data). Herring Gulls had slower but more efficient digestion than Common Murres when fed on two fish species that regularly occur in the diet of both species in the north-east Atlantic. Further, the two species' ecology differs considerably. Both species make discrete commuting trips to feeding sites which are removed from the nest territory. However Herring Gulls are generalist foragers, consuming a wide variety of food types, frequently including low quality items (low energy density or resistant to digestion) (Cramp and Simmons 1983). They have low wing loadings (Pennycuick 1987) and frequently use gliding flight, and so have relatively low flight energy expenditure (Pennycuick 1989). They carry large quantities of food back to a brood of up to three chicks which fledge at adult mass. By contrast, Common Murres are specialist piscivores, eating mainly small shoaling fish (Bradstreet and Brown 1985; Cramp 1985) which are relatively energy dense (Wallace and Hulme 1977; Montevecchi and Piatt 1984; Hislop *et al.* 1991) and easy to digest (Hilton *et al.* submitted ms). Their wing loading is among the highest of any flying bird (Pennycuick 1989), and they frequently make long flights to the feeding grounds (Bradstreet and Brown 1985; Phillips *et al.* in press). They carry only very small quantities of food back to a single chick which fledges at one third of adult mass (Harris and Birkhead 1985).

METHODS

In a study of eight North Atlantic seabird species, Hilton *et al.* (submitted ms) found a negative relationship between digestive efficiency, measured as Nitrogen-corrected true metabolisable energy coefficient ($TMEC_N$, Miller & Reinecke 1984), and mean retention time of digesta. We adapt this interspecific relation to approximate the likely trade-off within our model species.

For each of the eight species, a negative exponential curve was fitted to plots of cumulative wet excreta production against time after a meal, and from the fitted curves we calculated Δ , the specific excretion rate (percent wet meal mass excreted/second). $TMEC_N$ was related to Δ in the following relationship:

$$TMEC_N = 0.628 \times \Delta^{-0.043} \quad (F_{1,6} = 7.5; r^2 = 0.56; p = 0.03) \quad (1)$$

which was used in the model to define the resultant digestive efficiency for any given specific excretion rate.

Model overview

The model derives those combinations of number and duration of foraging trips which allow the bird to balance its energy budget over a 24 hour period, whilst delivering enough food to the chick(s). These combinations were calculated for a rapid digester (high specific excretion rate) and a slow digester (low specific excretion rate), under a range of plausible combinations of food energy density and foraging range. Thus we compare a hypothetical slow digesting Common Murre with a rapid digesting individual of the same species, and consider the impact on a Herring Gull of adopting a rapid digestion strategy versus a slow digestion strategy. We consider two separate optimisation criteria: firstly, “time minimisation”, in which the bird aims to minimise the time spent away from the nest, and secondly, “energy minimisation”, in which the bird aims to minimise its daily energy expenditure.

Optimisation criteria

Minimising time spent on feeding trips is a means of maximising time spent at the nest. This is likely to reduce the risk of chick predation - a major cause of mortality in both species (Hatchwell 1991; Bukacinska *et al.* 1996) - and strengthen pair bonds, which is an important behaviour in species such as these which pair for life

(Nelson 1988). Minimising daily energy expenditure is a means for an individual to maximise its residual reproductive value (Daan *et al.* 1990). When feeding conditions are favourable, Common Murres do not increase chick provisioning above the levels set in the model; instead they spend more time resting at the colony (Burger and Piatt 1990; Monaghan *et al.* 1994). This is consistent with the suggestion that once the threshold for healthy chick growth has been reached, they seek to minimise time away from the nest and/or their own energy expenditure.

Model definition

i) Strategy

The strategy of a pair of birds is defined by the number of feeding trips (n) which each bird makes, and its specific excretion rate (Δ). We assume that each bird in the pair makes the same number of trips. We further assume that the total time available to the pair for feeding trips (T) is 18 hours (=86,400 seconds) per day, since neither species regularly forages in darkness during the chick rearing period (Sibly and McLeery 1983; Harris and Wanless 1985). In Common Murres it is normal for one parent to attend the chick at all times (Wanless *et al.* 1988). Therefore in the model we allow each member of the pair nine hours per day in which to forage, and the birds alternate feeding trips. Time limits are less strict for Herring Gulls: pairs of this species with large chicks often leave them unattended, so we allow each member of the pair up to 18 hours per day of feeding trip time.

Thus for Common Murres, trip durations cannot exceed t_{max} seconds, where

$$t_{max} = \frac{T}{2n}. \quad (2)$$

If we measure time of day (t_{day}) starting from dawn, then one bird will begin its trips at times $t_{day} = 0, 2t_{max}, 4t_{max}$ etc., whereas its partner will begin at $t_{day} = t_{max}, 3t_{max}$ etc. This alternation will continue until one bird is due to leave at time $t_{day} = T$.

For Herring Gulls, trip durations cannot exceed

$$t_{max} = \frac{T}{n}. \quad (3)$$

ii) Energy needs

Let us assume that the daily energy requirements of the brood is given by a constant E_{chick} , and the daily requirements of an adult which remains at the nest are given by E_{adult} (both measured in kJ). We assume that on each feeding trip sufficient assimilable energy is gathered to cover the extra costs incurred during the feeding trip and to gather extra energy equivalent to

$$\frac{E_{chick}}{2n} + \frac{E_{adult}}{n}. \quad (4)$$

The extra energy costs of the feeding trip can be broken down into the flight costs of commuting to and from the foraging grounds, and the costs incurred at the feeding site.

iii) Outward flight

The extra power required for powered flight with different payloads can be calculated from Pennycuik (1989). A key component of our model is that flight costs are a function of mass. Specifically, for a Common Murre of mass W (g), the cost of flapping flight (in Watts) is given by

$$F(W) = 0.0018W^{1.6}. \quad (5)$$

For Herring Gulls, this becomes

$$F(W) = 0.0012W^{1.5}. \quad (6)$$

Further, we assume that, whilst Common Murres use flapping flight exclusively, Herring Gulls flap for 50% of the time and glide for the remainder (Norstrom *et al.* 1986). The energy costs of gliding flight are generally considered to be twice the resting metabolic rate (RMR) (Baudinette and Schmidt-Nielsen 1974). Hence, the actual costs of flight in a Herring Gull are given by

$$F(W) = 0.0006W^{1.5} + RMR. \quad (7)$$

We assume that every time a bird begins its foraging trip, all food from previous trips has been processed, so the bird's mass is simply a constant "empty mass" W_e . Thus, if the foraging area is a distance D (km) from the nest, and the bird flies at a constant speed V (in m/s), then the extra energy used in the outbound flight, E_{out} (kJ) is given by

$$E_{\text{out}} = \frac{F(W_c)D}{V}. \quad (8)$$

iv) *Feeding and excretion rates*

Whilst at the feeding site, the bird eats food at a rate S (g/second). As it forages, the mass of food it carries (W_f) increases. If the mass of food carried is lower than maximum capacity of the gut (W_{max}), then the feeding rate is unconstrained by digestive considerations and proceeds at a constant rate (S_{max}). However, if the birds' digestive tract is full, then it is forced to ingest food at a (generally lower) rate equivalent to the rate at which mass is excreted.

In order to describe time at the feeding site (t seconds), we now define the time that the bird arrives at the feeding site as $t = 0$. The bird begins filling its digestive tract at this time. However, no food is excreted until after a fixed (transit) time t_{transit} (estimated from direct observation during digestion trials to be 60 minutes for Herring Gull and 70 minutes for Common Murre). After this time, the excretion rate (in g/s) is given by the product of the mass of food in the digestive tract (W_f), and the specific excretion rate (Δ) defined earlier. Mathematically, we can define the feeding rate as follows:

$$S = \left\{ \begin{array}{ll} S_{\text{max}}, & \text{if } w_f < w_{\text{max}} \\ 0, & \text{if } w_f = w_{\text{max}} \text{ and } t < t_{\text{transit}} \\ S_{\text{min}}, & \text{if } w_f = w_{\text{max}} \text{ and } t \geq t_{\text{transit}} \end{array} \right\} \quad (9)$$

where $S_{\text{min}} = \Delta \times W_f$.

The amount of food in the digestive tract starts at zero, when $t = 0$, and changes as follows:

$$\frac{dW_f}{dt} = \left\{ \begin{array}{ll} S, & \text{if } t < t_{\text{transit}} \\ S - S_{\text{min}}, & \text{if } t \geq t_{\text{transit}} \end{array} \right\}. \quad (10)$$

v) *Cost of foraging*

We can also calculate the extra energy spent at the feeding site (E_{forage}) (kJ). We assume that the bird divides its time between resting on the water (which costs an extra R_{water} Watts above RMR) and actively feeding (which costs an extra R_{feeding}

Watts above RMR). Specifically, E_{forage} starts at zero when $t = 0$, and increases as follows:

$$\frac{dE_{forage}}{dt} = \frac{R_{water} + \frac{S(R_{feeding} - R_{water})}{S_{max}}}{1000}. \quad (11)$$

vi) *Flight back to nest*

We need to calculate the cost of the homeward flight. This is more complicated than for the outbound trip because an individual's mass will decrease through excretion during the flight. If the bird leaves the feeding site at a time t_L (measured from the point of arrival), then the energy cost of the homeward flight (in kJ) will be given by

$$E_{back} = \frac{\int_{t_L}^{t_L + \frac{D}{v}} F(W_e + W_f(t)) dt}{1000} \quad (12)$$

where, from time t_L , W_f changes according to

$$\frac{dW_f}{dt} = \begin{cases} 0, & \text{if } t < t_L \\ -S_{min}, & \text{if } t \geq t_L \end{cases}. \quad (13)$$

vii) *Energy gathered*

The last quantity we need to define is the total energy gathered during a feeding period (E_{in}) in kJ. This starts at zero when the bird arrives at the feeding site ($t = 0$), and increases according to

$$\frac{dE_{in}}{dt} = \begin{cases} QS, & \text{if } E_{in} < E_{chick} \\ eQS, & \text{if } E_{in} \geq E_{chick} \end{cases} \quad (14)$$

where Q is the energy density of the food (kJ/g wet mass) and e is $TMEC_N$ ($0 < e < 1$). The energy which the bird gathers for the chick is not assimilated, so is not subjected to losses incurred in this process. In reality the bird would likely gather this food for the chick at the end of its feeding period. Here, for mathematical convenience, it is gathered at the start; this has no effect on the model's predictions.

viii) *Time spent at feeding site*

Armed with the foregoing, we can calculate the energy gathered (E_{in}) for any given time interval at the feeding site (t). We have also calculated the fixed energy requirements (E_{adult} , E_{chick} and E_{out}) and the costs of feeding for a time (t), $E_{forage}(t)$ and of flying back to the nest after this time, $E_{back}(t)$. We find the unique value of t (t^*) where the individual gathers exactly enough energy to cover its costs: i.e. we solve

$$E_{in}(t^*) = \frac{E_{adult}}{n} + \frac{E_{chick}}{2n} + E_{out} + E_{forage}(t^*) + E_{back}(t^*). \quad (15)$$

Providing that the bird can gather assimilable energy faster than it expends energy during foraging, this equation has a unique solution: this is the time which we assume the bird spends at the feeding site. We find this time for a range of daily feeding trip numbers (n). We then find the set of values of n for which the trip can be accomplished within the time limit: i.e. for which

$$t^* + \frac{2D}{V} \leq t_{max}. \quad (16)$$

From this subset we find the value of n which optimises one of our two criteria (see earlier). This is the optimal strategy, for which we determine the time spent foraging, and the energy expended over a whole day.

ix) An alternative energy minimising strategy - "sit and wait"

Consider an alternative strategy whereby the bird saves flight energy costs on the return journey to the nest by sitting on the water for as long as it can before flying back to the nest just within the maximum trip duration restriction. If the individual forages for a time t , then it can wait on the water for a time

$$t_{max} - t - \frac{2D}{V}, \quad (17)$$

before flying back. We assume that there is an added cost (measured in kJ) to resting on the water compared to the protected micro-climate of the nest. This is given by

$$E_{sit} = R_{water} \left(t_{max} - t - \frac{2D}{V} \right). \quad (18)$$

However, the bird's flight energy costs will be reduced because it will have been losing mass according to equation (13) during the time that it remained on the water

at the feeding site. As before, we find the unique foraging time (i.e. time interval from arriving in the foraging area to finally quitting feeding) t^* , under the assumption that the bird will then sit on the water as long as possible before flying back. This t^* is obtained by solving

$$E_{in}(t^*) = \frac{E_{adult}}{n} + \frac{E_{chick}}{2n} + E_{out} + E_{forage}(t^*) + E_{sit} + E_{back}(t^*). \quad (19)$$

Model runs

For Common Murres, model runs simulate commonly observed foraging ranges (D) of 0 - 100 km, food energy densities (Q) of 4 - 8 kJ/g wet mass, and maximum ingestion rates (S_{max}) of 0.037 g/sec. For Herring Gulls these parameters become D = 0 - 30 km, Q = 3 - 7 kJ/g wet mass, and $S_{max} = 0.067$ g/sec. Appendix 1 gives published information on plausible foraging conditions, and other parameter values adopted in the model. For each species and set of foraging circumstances we consider both a slow ($\Delta = 0.0015$ percent meal mass/sec) and a rapid ($\Delta = 0.011$ percent meal mass/sec) digestion strategy. This corresponds to the range of values observed in our experimental studies, and allows $TMEC_N$ to vary between 0.76 and 0.83.

RESULTS

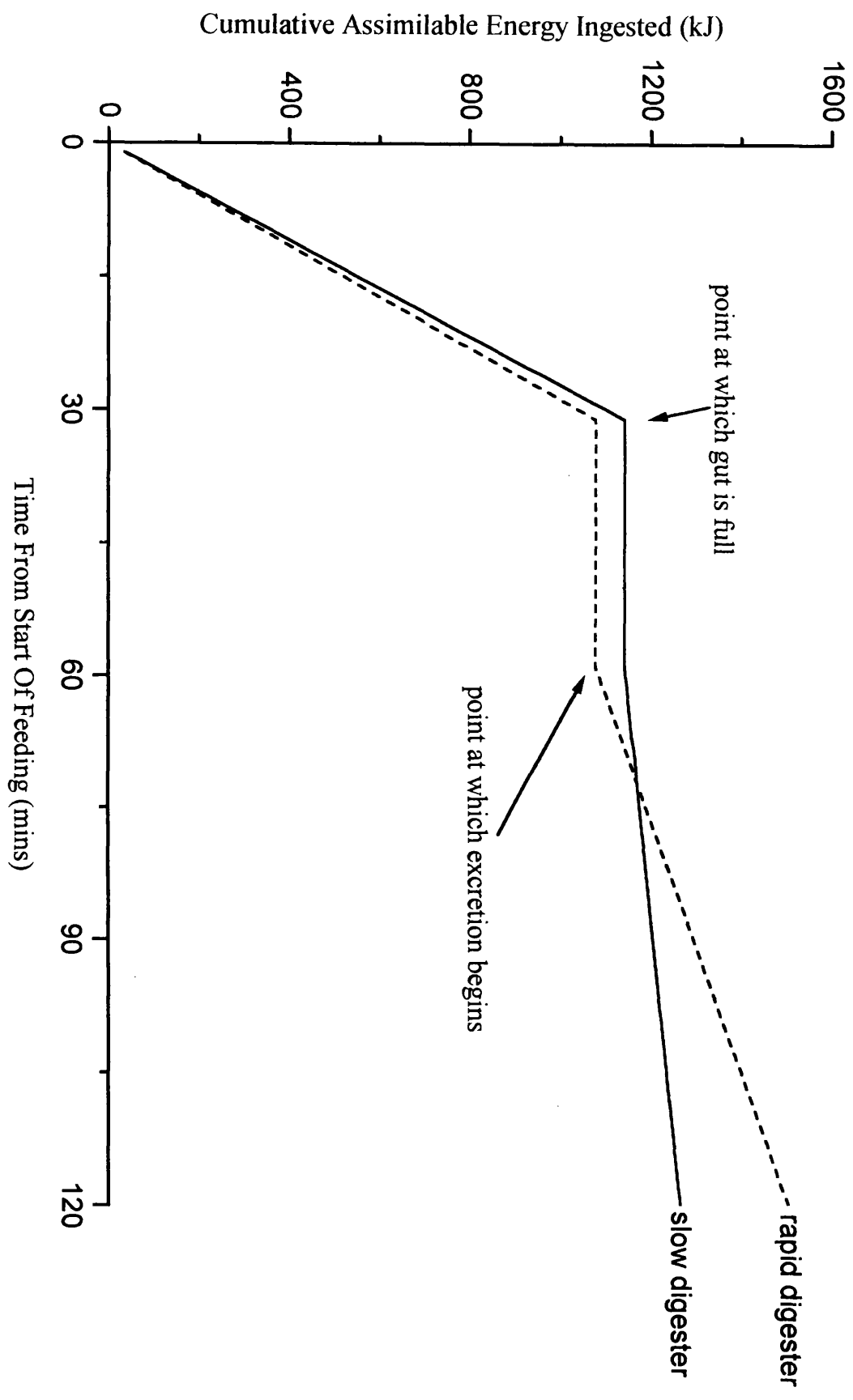
Patterns of energy gain

Figure 3.1 compares the cumulative assimilable energy gain of a slow digester with a fast digester over the course of a feeding period, and is key to the outcomes of the model. Initially, the rate of energy gain is determined by the rate at which food can be ingested, and the efficiency with which that food is digested. During this period, energy gain is rapid for both strategies, but is slightly higher for the slow digester, because it has higher digestive efficiency. This period of rapid energy gain continues until the gut is full. From this point, food can only be ingested if space is created in the gut by excretion, and therefore ingestion rate is limited by excretion rate. If gut fill is reached before excretion starts, then ingestion must cease completely until excretion commences. Thereafter, ingestion rate is equal to excretion rate. The crucial point is that the rate of excretion of both fast and slow digesters is much lower than the unconstrained rate of ingestion. Thus, following gut fill there is a major “ingestion bottleneck” on energy assimilation, and the severity of this bottleneck is determined by the excretion rate: its impact is much greater for slow digesters than for fast digesters.

Time minimisation

For any digestion strategy there are two key behavioural strategies which aid the minimisation of daily foraging time. Firstly, birds should avoid the ingestion bottleneck by terminating feeding periods at or before gut fill, since after gut fill energy gain is relatively slow, and therefore this is a very time-inefficient feeding situation. Secondly, each feeding trip incurs a fixed time penalty - flight time between nest and feeding grounds - so that infrequent trips with long feeding periods should be favoured. There is, however, conflict between these two strategies; the former favouring a limited feeding period on each trip, and the latter favouring long feeding periods. The optimal strategy balances these pressures to give the shortest possible time away from the nest.

Fig 3.1: Cumulative energy assimilation curves during a feeding period for a low excretion rate and a high excretion rate strategy.



Where the balance lies is dependent on both the digestion strategy and the foraging conditions. Figures 3.2a and 3.2b show the optimal number of feeding trips per day for rapid and slow digesting Common Murres and Herring Gulls eating high and low quality food, at a range of foraging distances. Feeding trip frequency decreases as food energy density increases, simply because less food must be gathered in order to assimilate the required amount of energy. Avoidance of the ingestion bottleneck is more important for slow digesters, and therefore they tend to make more and shorter feeding trips than rapid digesters under many combinations of food energy density and foraging range. Under foraging conditions where rapid digesters do make fewer trips, rapid digestion is almost always the time minimising strategy (Figure 3.3a, 3.3b). Under those foraging conditions where the optimal trip frequency does not differ between digestion strategies then slow digestion is the time minimising strategy, but by small margins only.

For Common Murres, rapid digestion is the time minimising strategy under most realistic foraging conditions, often by a large margin of up to 200 minutes per day (Figure 3.3a). For Herring Gulls slow digestion is the time minimising strategy when foraging conditions are more favourable (high food energy density and/or short foraging range), and rapid digestion is favoured when conditions are more severe, but the difference between the strategies is never more than about 50 minutes, and rarely more than 15 minutes (Figure 3.3b).

As foraging conditions deteriorate (foraging range increases and food energy density decreases), the minimum time away from the nest increases until a threshold is reached beyond which the bird is unable to achieve energy balance within the time available. It must presumably then either use body reserves to meet the energy deficit or neglect the chicks. An important outcome of the model is that rapid digesters achieve energy balance within the time limit under more severe foraging conditions than slow digesters. This is illustrated in Figure 3.4, which shows the threshold foraging range - food quality combinations for fast and slow digesting Common Murres. For Herring Gulls we assumed that the absolute limit to daily foraging time is 18 hours (see methods), and this time limit was exceeded only under the harshest of foraging conditions.

Fig 3.2: Optimal feeding trip frequency for minimising daily foraging time, as a function of foraging range.

(a) Common Murre.

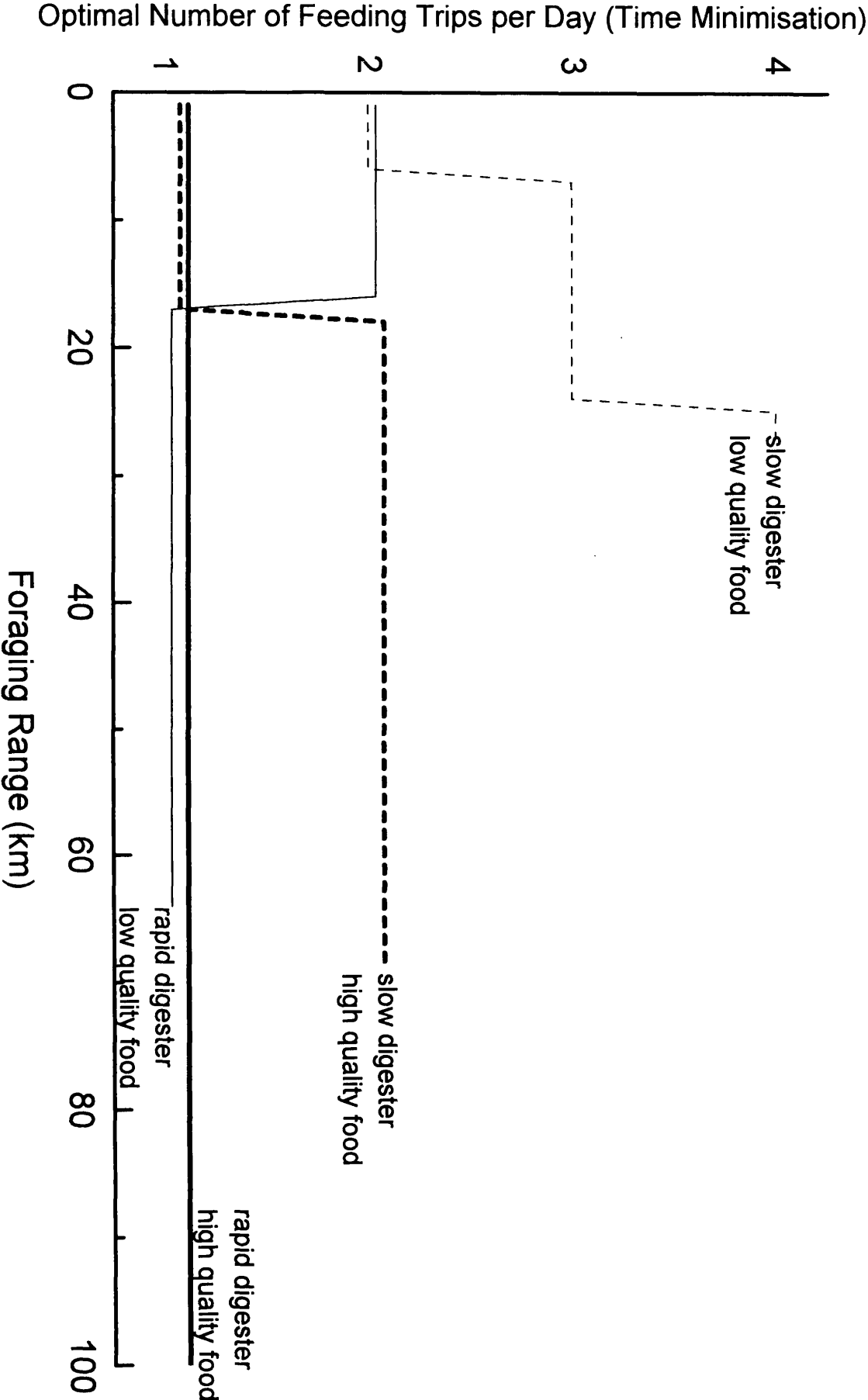
Dashed line: slow digestion ($\Delta = 0.0015$); solid line: rapid digestion ($\Delta = 0.011$).

Narrow lines: low quality food (4 kJ/g); thick lines: high quality food (8 kJ/g).

(b) Herring Gull.

Dashed line: slow digestion ($\Delta = 0.0015$); solid line: rapid digestion ($\Delta = 0.011$).

Narrow lines: low quality food (3 kJ/g); thick lines: high quality food (7 kJ/g).



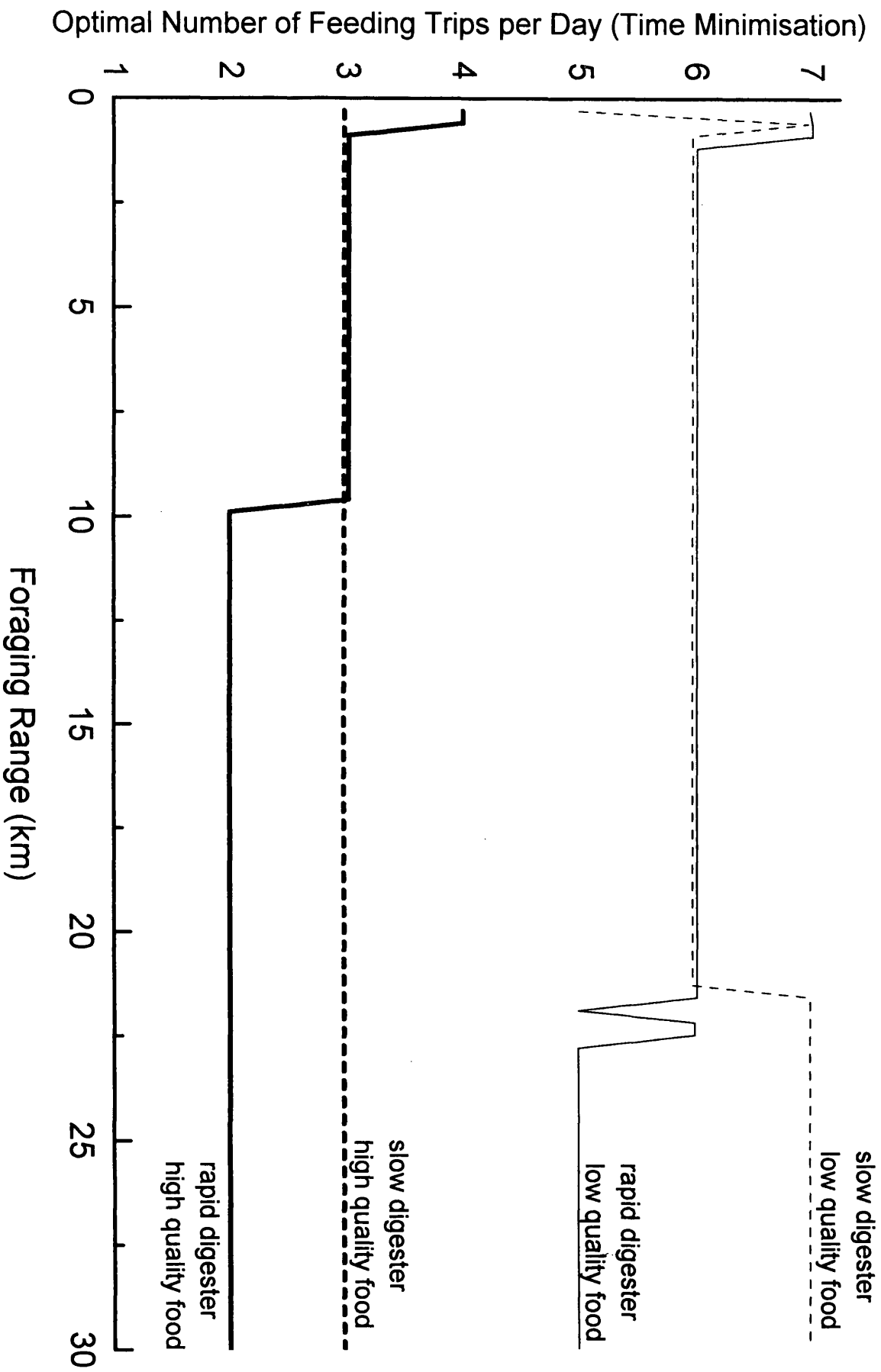


Fig 3.3: Minimum daily foraging time as a function of foraging range.

(a) Common Murre.

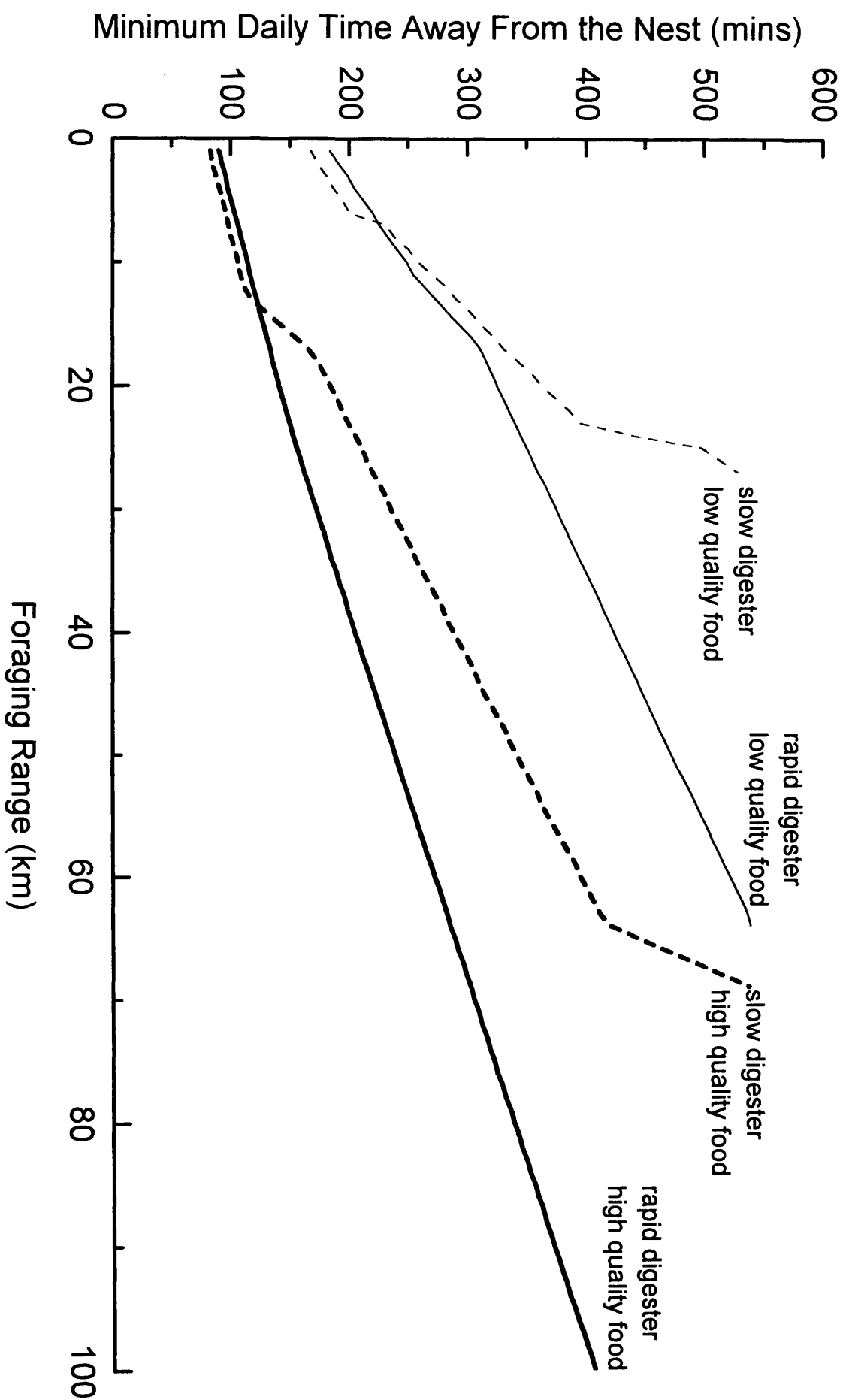
Dashed line: slow digestion ($\Delta = 0.0015$); solid line: rapid digestion ($\Delta = 0.011$).

Narrow lines: low quality food (4 kJ/g); thick lines: high quality food (8 kJ/g).

(b) Herring Gull.

Dashed line: slow digestion ($\Delta = 0.0015$); solid line: rapid digestion ($\Delta = 0.011$).

Narrow lines: low quality food (3 kJ/g); thick lines: high quality food (7 kJ/g).



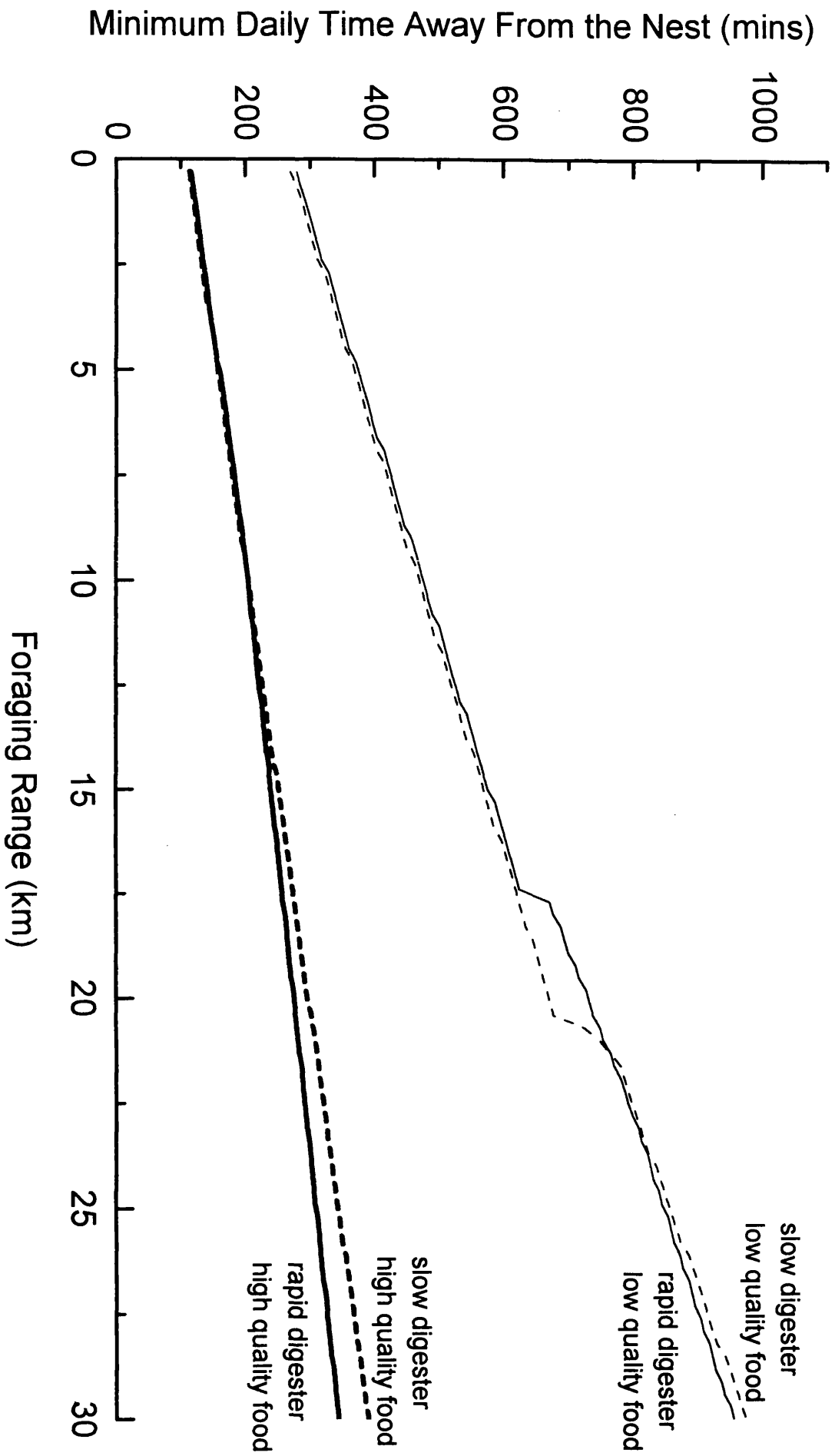
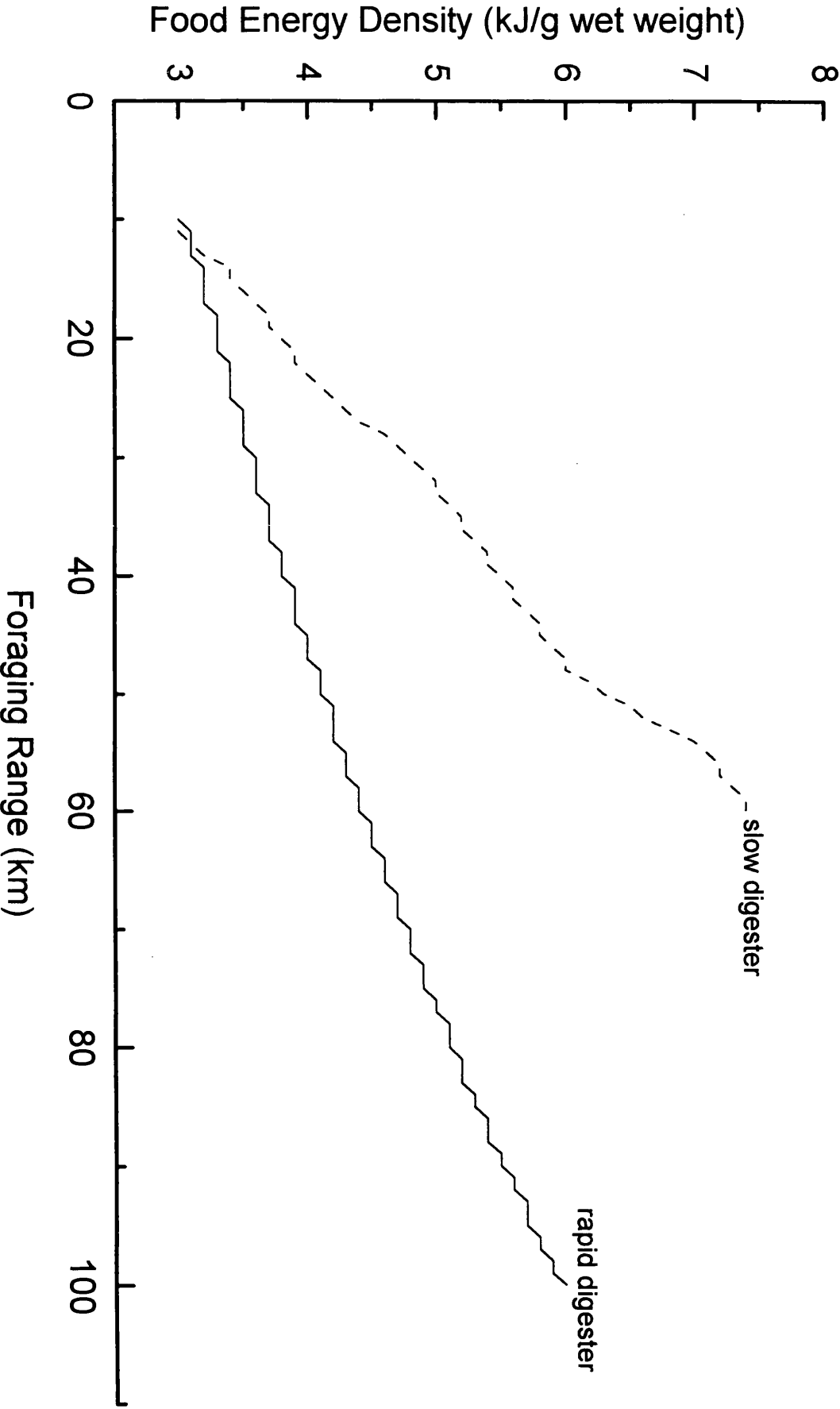


Fig 3.4: Threshold combinations of food energy density and foraging range for achieving energy balance in the Common Murre, as a function of digestion strategy.

The curves depict the food energy density - foraging range combinations at which the bird meets energy balance in 540 minutes, the daily time available for foraging. At greater foraging ranges, and/or lower food energy densities, the bird must neglect the chick or accept negative energy balance.

Dashed line: slow digestion ($\Delta = 0.0015$); solid line: rapid digestion ($\Delta = 0.011$).

The rapid digester is able to achieve energy balance under much more severe foraging conditions.



Energy minimisation

When the minimisation of energy expenditure is the optimisation criterion, the optimal feeding trip frequency is always the lowest that can be achieved within the constraints of chick provisioning. This is because for each feeding trip made there is a fixed energy cost - the cost of flying to the feeding site. In contrast to the time minimising strategy, there is almost no cost associated with continuing to feed after the ingestion bottleneck sets in. The difference arises because we assume that when the bird is constrained to reduce its ingestion rate to equal the rate of excretion, it spends the “spare” time at the feeding site resting on the water surface, which is only marginally more energetically expensive than resting at the nest site (Croll and McLaren 1993).

The number of feeding trips per day for energy minimisation frequently exceeds one however. If all the daily energy requirements are gathered on a single feeding trip, then a large amount of food must be ingested on that trip, which tends to mean that the feeding period is continued well after the onset of the ingestion bottleneck. Doing this is so time-inefficient that it frequently results in the bird exceeding the maximum daily time away from the nest (nine hours and 18 hours for Common Murre and Herring Gull respectively). Thus more and shorter feeding trips must be made in order to avoid the ingestion bottleneck and meet the time constraints. Also, for the Herring Gull it is often not possible to carry the entire chick requirements in a single load, due to gut capacity limitations, so extra feeding trips must be made purely to maintain chick provisioning.

As discussed above, rapid digesters have a higher energy assimilation rate after the ingestion bottleneck sets in. This means that for a given feeding trip frequency, the rapid digester is more likely than the slow digester to be able to achieve energy balance before the time limit is reached, and so avoid having to make an extra feeding trip. Rapid digestion is the energy minimising strategy by a considerable margin in those circumstances where the rapid digester is able to make fewer feeding trips than the slow digester. This is illustrated in Figures 3.5 and 3.6, which show optimal number of feeding trips for energy minimisation, and minimum daily energy expenditure, for the two species.

There is, however, a counter advantage to slow digestion. The increased digestive efficiency of this strategy means that less food must be ingested in order to assimilate the same amount of energy. This can result in energy savings, because less effort must be expended in foraging for that food. Thus under foraging conditions where minimum feeding trip frequencies are the same for both fast and slow digesters, slow digestion is the energy minimising strategy, but by small amounts only.

The model runs indicate that rapid digestion is likely to be favoured for energy minimisation in the Common Murre, except where food is high quality and foraging range small (Figure 3.6a). However, under most circumstances slow digestion is the energy minimising strategy for the Herring Gull, the exception to this being under conditions of low food quality and long foraging range (Figure 3.6b).

Lastly, for Common Murres we explored another potential energy minimising strategy, which we term "sit and wait". Figure 3.7 illustrates the energy savings that can be made by operating this strategy, as compared to simply flying back to the nest immediately the feeding period ends (which is the situation we have modelled in the time minimising and energy minimising sections). The energy savings are proportional to the foraging range, and for the larger foraging ranges are considerable, up to around 10% of daily energy expenditure.

Fig 3.5: Optimal feeding trip frequency for minimising daily energy expenditure, as a function of foraging range.

(a) Common Murre.

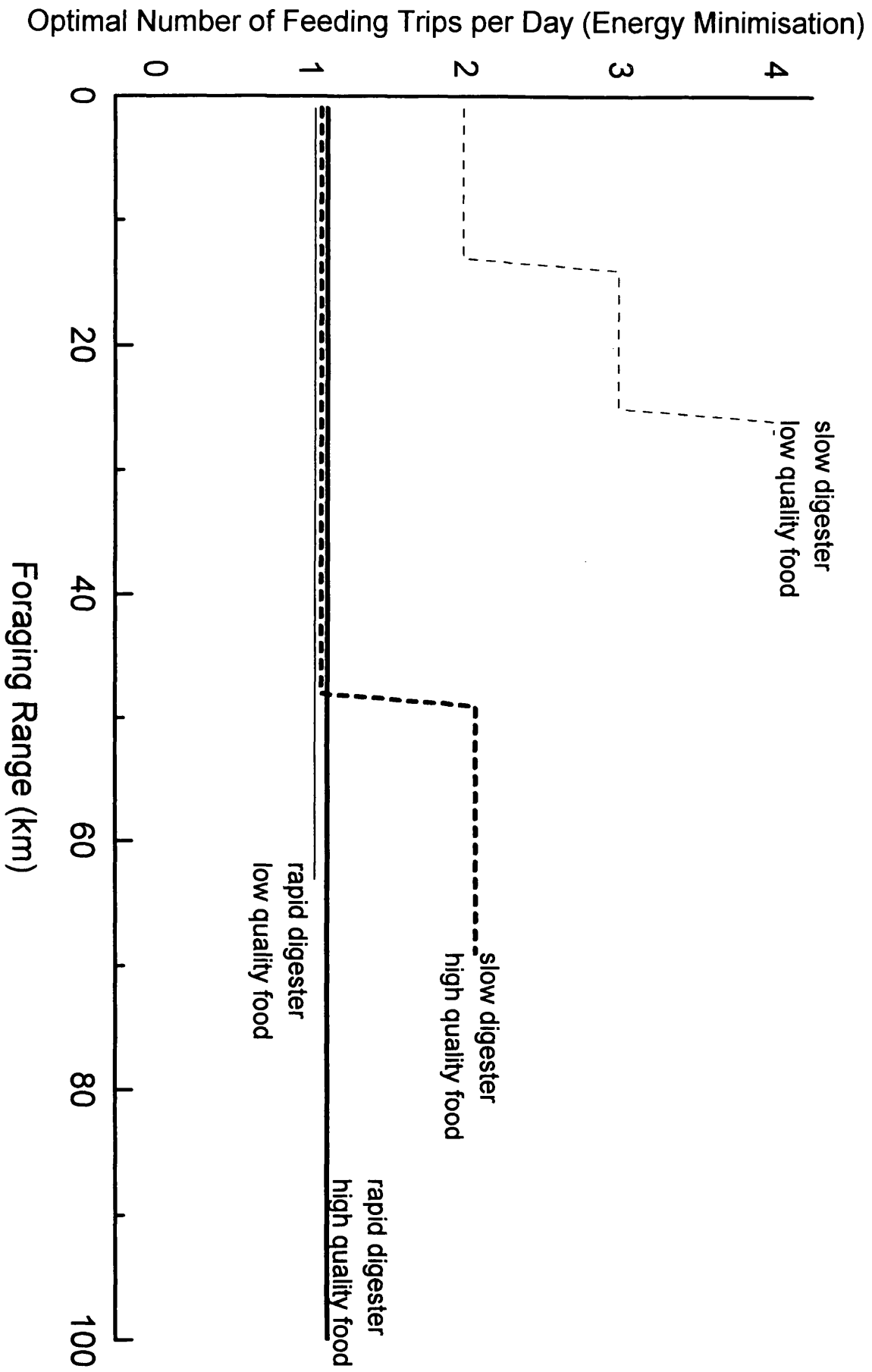
Dashed line: slow digestion ($\Delta = 0.0015$); solid line: rapid digestion ($\Delta = 0.011$).

Narrow lines: low quality food (4 kJ/g); thick lines: high quality food (8 kJ/g).

(b) Herring Gull.

Dashed line: slow digestion ($\Delta = 0.0015$); solid line: rapid digestion ($\Delta = 0.011$).

Narrow lines: low quality food (3 kJ/g); thick lines: high quality food (7 kJ/g).



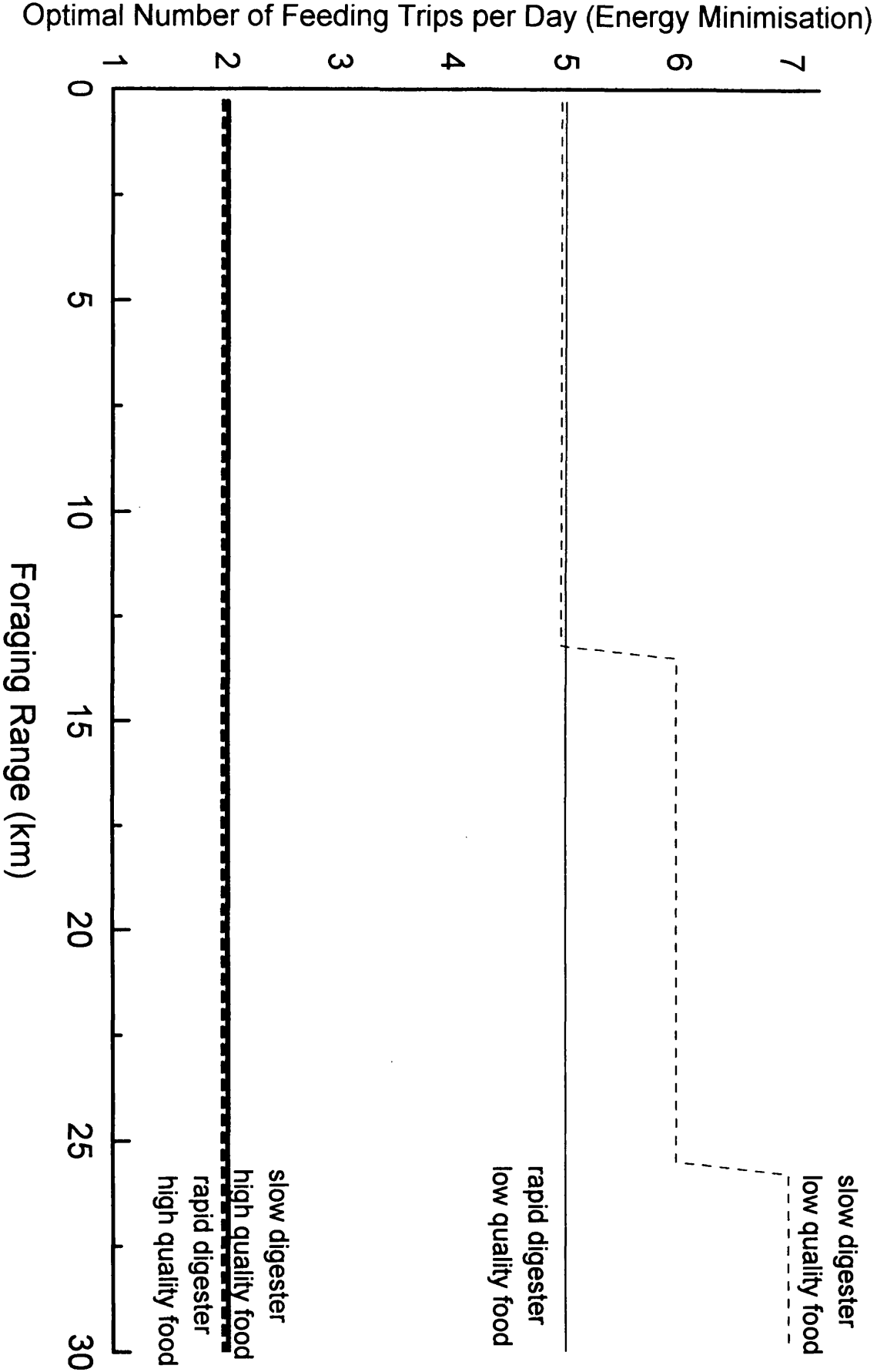


Fig 3.6: Minimum daily energy expenditure as a function of foraging range.

(a) Common Murre.

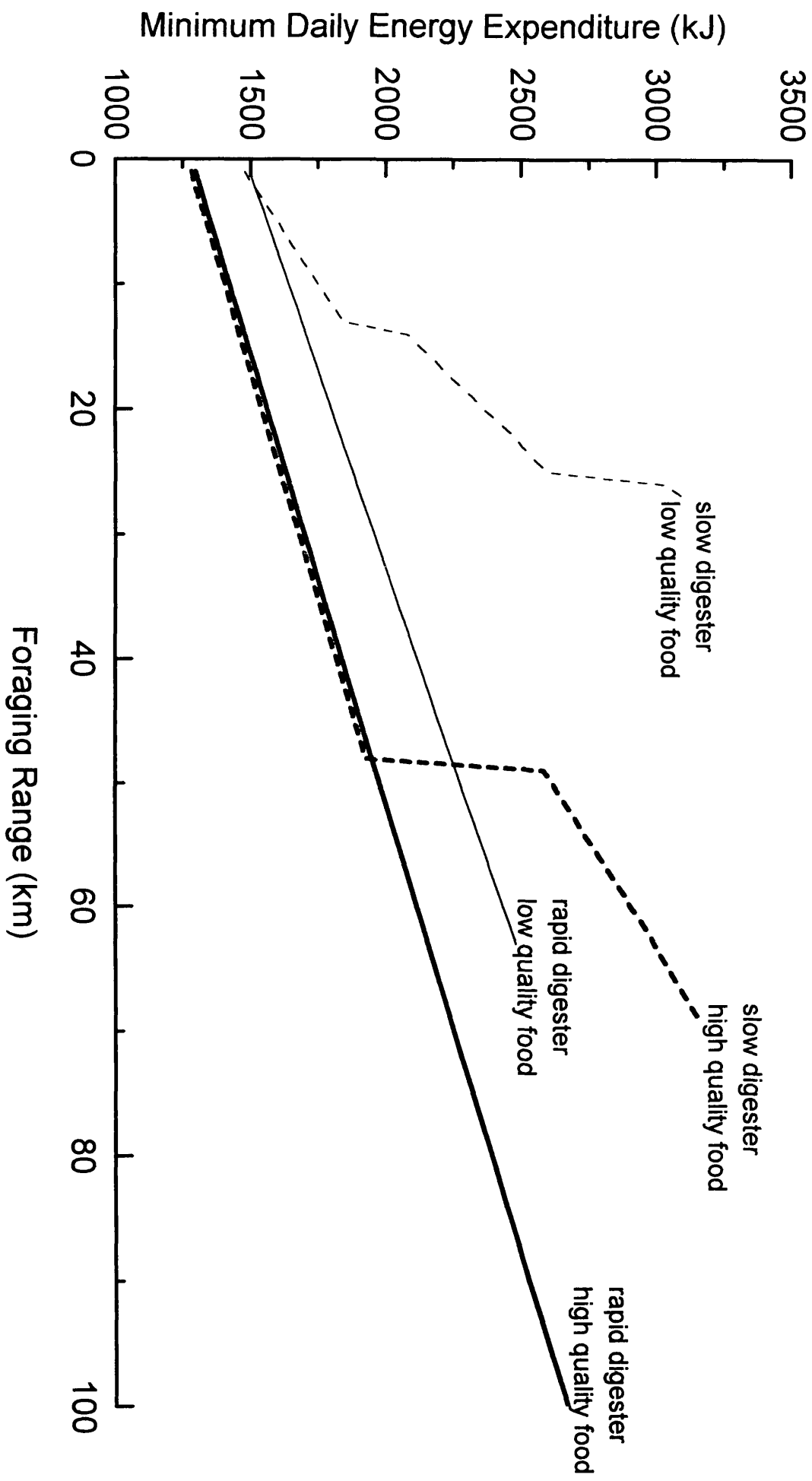
Dashed line: slow digestion ($\Delta = 0.0015$); solid line: rapid digestion ($\Delta = 0.011$).

Narrow lines: low quality food (4 kJ/g); thick lines: high quality food (8 kJ/g).

(b) Herring Gull.

Dashed line: slow digestion ($\Delta = 0.0015$); solid line: rapid digestion ($\Delta = 0.011$).

Thin lines: low quality food (3 kJ/g); thick lines: high quality food (7 kJ/g).



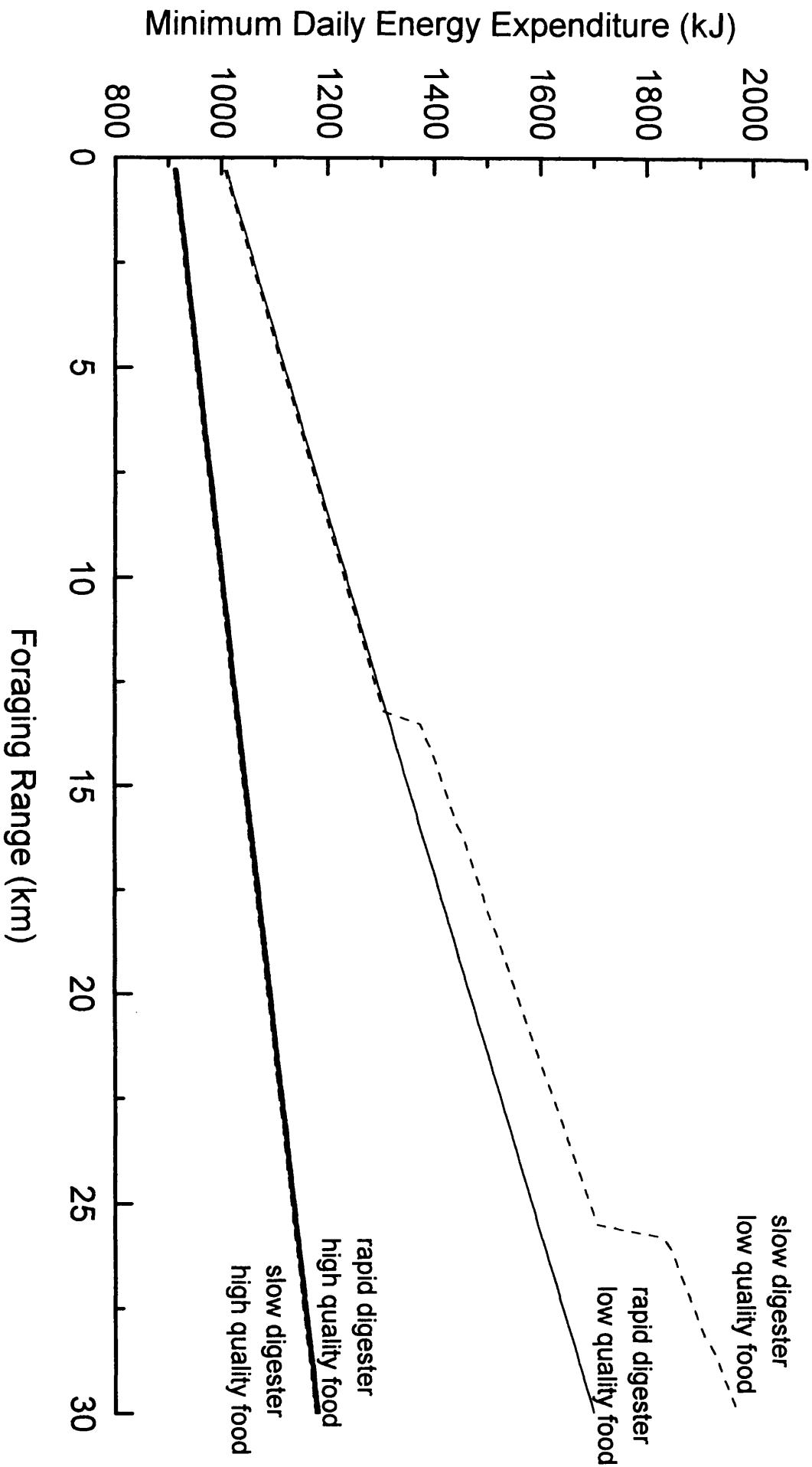
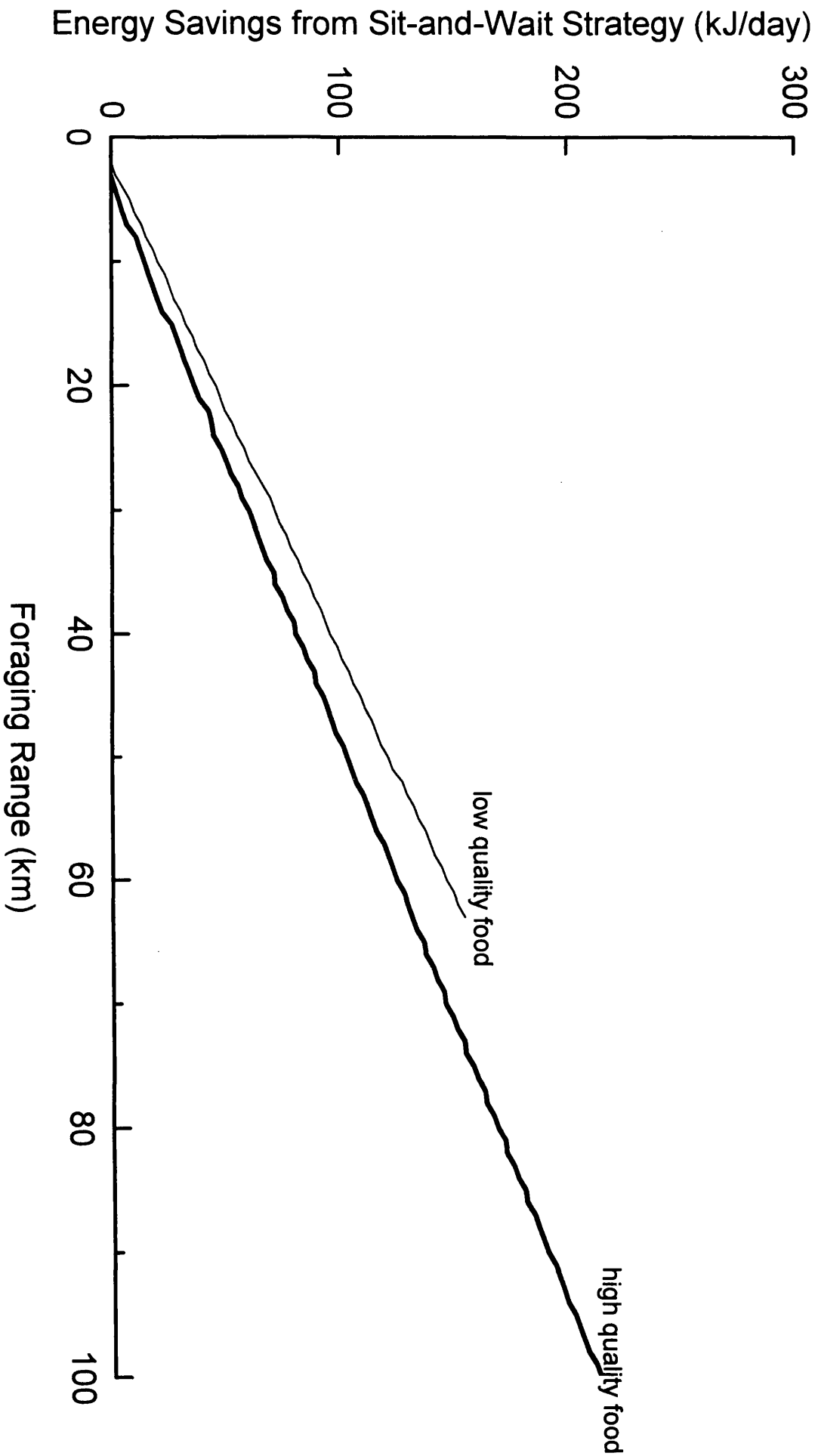


Fig 3.7: Daily energy savings that can be achieved by Common Murres adopting the "sit-and-wait" strategy.

Values are kJ per day saved, compared to adopting a conventional energy minimising strategy of flying back to the nest immediately the foraging period ends.

Dashed line: low quality food (4 kJ/g); solid line: high quality food (8 kJ/g). Both curves represent rapid digestion.



DISCUSSION

Which digestion strategy is favoured ?

The model successfully predicts that, as was observed in digestion trials (Hilton *et al.* submitted ms), rapid digestion is optimal for Common Murres. For this species, the only times when slow digestion appears to be favoured are under conditions of very high food quality coupled to a small foraging range. Model predictions suggest that under demanding foraging conditions this species may find it difficult to gather enough energy in the time available for foraging, and that therefore a time minimising rapid digestion strategy will be very strongly selected. We have also shown that, as Gabrielsen (1996) proposed, a "sit-and-wait" strategy of remaining at the feeding site for as long as possible can save energy expenditure, because excretion of part of the ingested food reduces flying mass.

By contrast, according to the model neither strategy is clearly better for the Herring Gull, which had longer retention times in digestion trials (Hilton *et al.* submitted ms). For both optimisation criteria there is a tendency for slow digestion to be favoured when foraging conditions are favourable, and for rapid digestion to be favoured when conditions are more severe.

Other factors affecting favoured digestion strategy

Energy assimilation bottlenecks

There has been much interest in the idea that the processing capacity of the gut sets an upper limit to the amount of food an animal can eat, and therefore to the energy that an animal can metabolise (Kirkwood 1983; Weiner 1989, 1992; Suarez 1996; Hammond and Diamond 1997). The Common Murre has a high food quantity requirement because it has a high daily energy expenditure (Cairns *et al.* 1987; Gabrielsen 1996), while the Herring Gull must frequently have a high food requirement because it eats food of low energy density (Pons 1994; Pierotti and Annett 1987). If an animal has a high food processing requirement then either gut capacity must be increased, or gut retention time must be decreased (Karasov 1996). Is it therefore possible that digestion rate of our modelled species is influenced by processing capacity limitations?

Following Kersten and Visser (1996), we calculated the maximum energy assimilation of our study species as a function of their excretion rate. To calculate the mass of food processed, we assumed that over the whole day the gut was kept on average half-full, i.e. containing approximately 100 ml of digesta. Thus daily mass of excreta produced is the specific excretion rate (percent meal mass excreted/sec) x 100 ml x 86,400 seconds. The mean asymptotic proportion of wet meal mass excreted by seabirds species in digestion trials was 0.60 (s.d. = 0.14), so total wet mass of food processed (g) is mass excreted/0.6. Energy assimilated (kJ) from this food mass is

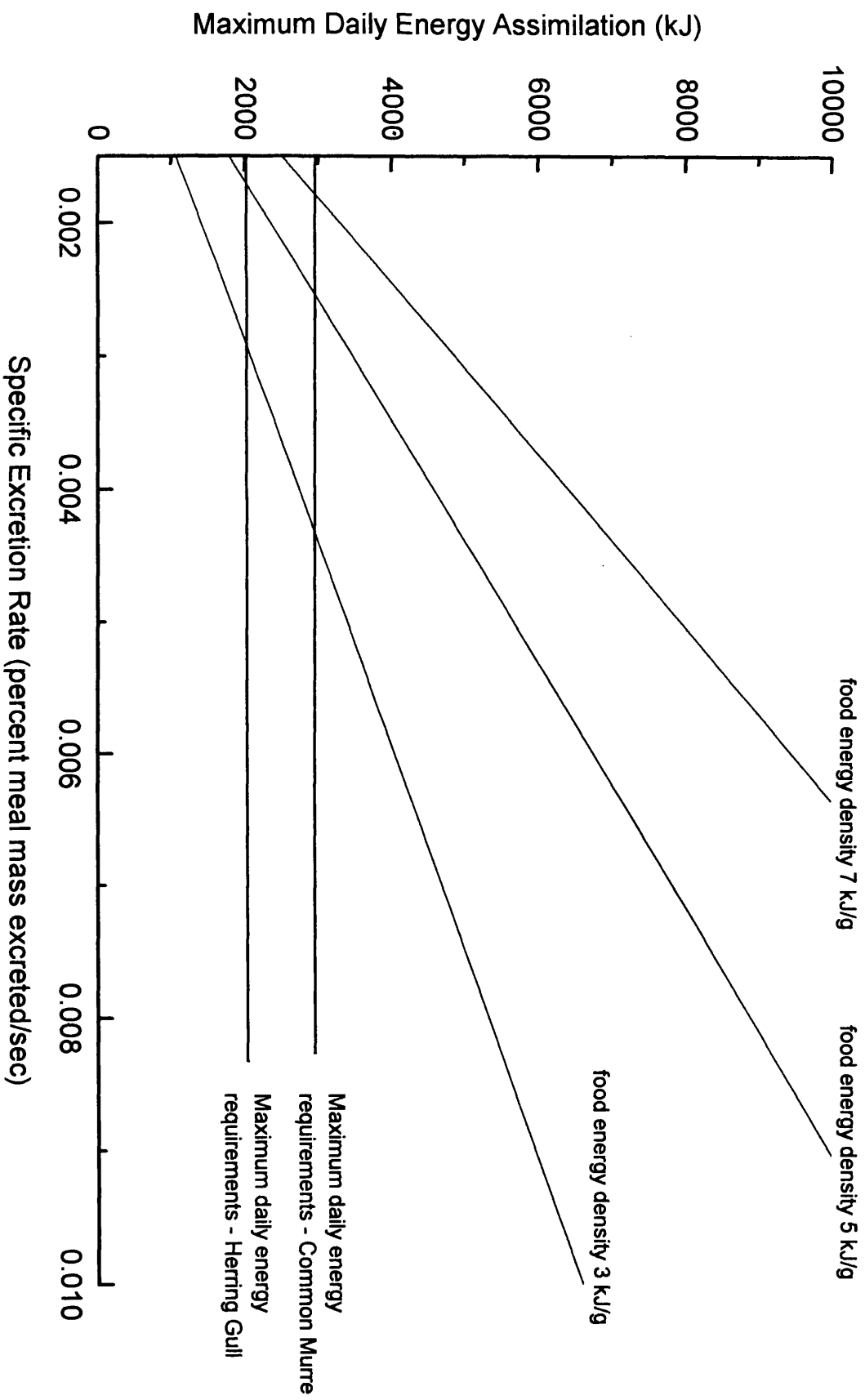
$$\text{food processed} \times \text{food energy density} \times \text{digestive efficiency} \quad (20)$$

where digestive efficiency is TMEC_N , calculated from the excretion rate - digestive efficiency trade-off curve.

The models predicted maximum daily energy requirements under harsh foraging conditions of around 2,000 kJ per day for Herring Gulls and 3,000 kJ per day for Common Murres (Figure 3.6). Figure 3.8 shows the calculated maximum daily energy assimilation, as a function of specific excretion rate, for three different food energy densities. When specific excretion rate is very low, daily energy assimilated is below predicted energy requirements, especially where food energy density is low. Avoiding an energy assimilation bottleneck may therefore be a factor in selecting against the slowest excretion rates. However, except in these rather exceptional circumstances, maximum energy assimilation seems to exceed energy requirements by a fairly large margin.

Fig 3.8: Maximum daily energy assimilation (kJ) as a function of specific excretion rate, for three different food energy densities.

Horizontal lines at 2,000 and 3,000 kJ indicate approximate maximum daily energy requirements of Herring Gulls and Common Murres respectively, taken from the energy minimising model outcomes. Where maximum daily energy requirements exceed maximum daily energy assimilation then an energy assimilation bottleneck may occur.



Prey capture rate and temporary flightlessness

Barton and Houston (1994) argued that pursuit-foraging raptors adopt a rapid digestion strategy because their flight performance, and hence their hunting ability, is strongly mass dependent (Andersson and Norberg 1981), and rapid excretion is a means of rapidly reducing mass after a meal (Sibly 1981). This selection pressure on pursuit predators is distinct from those that we have modelled. However, its importance in seabirds is unclear: the effect of mass on underwater pursuit performance as practised by the Common Murre are entirely unknown; Herring Gulls rely little on flight or diving performance for their foraging success.

Birds such as the Common Eider, *Somateria mollissima*, which eat very heavy meals relative to their body mass, and/or have small load carrying abilities may potentially be rendered temporarily flightless after feeding (Guillemette 1994). In this case there may be strong selection pressure to digest food rapidly. Wing loadings of Common Murres are among the highest recorded in flying birds (Pennycuik 1987), and they are further disadvantaged by the task of taking off from water, suggesting that temporary flightlessness may occur in this species. Herring Gulls, with much lower wing loading than Common Murres, are unlikely to be flightless even when the gut is filled to capacity.

Model assumptions

Our excretion rate - digestive efficiency trade-off curve is derived from an interspecific relationship among seabird species eating only two fish types. It may be unrealistic to assume that the relationship would take a similar form intraspecifically, or for different diets. Although an intraspecific relationship between retention time and digestive efficiency has been demonstrated by experimental manipulations of diet (Levey and Karasov 1992; Afik and Karasov 1995), the relationship has not been quantified.

Conclusions

The driving force behind the often large differences in time and energy budgets between different digestion strategies is the ingestion bottleneck that arises when the gut is full. It is the same phenomenon, but distinct in its effects, as the digestive bottleneck which limits energy assimilation in several taxa e.g. hummingbirds

(Diamond *et al.* 1986) and pigeons (Kenward and Sibly 1977), by enforcing resting periods between feeding bouts, in order to clear the gut. Here we have shown that such bottlenecks can have a profound influence on time and energy budgets, quite apart from simply constraining the maximum energy assimilation rate. The reason for this is the extreme time-inefficiency of prolonging feeding bouts once the gut is full. The onset of the bottleneck could be delayed by increasing gut capacity, but presumably this also would have costs: flying mass would be higher, causing greater energy expenditure (Pennycuick 1989), and the metabolic cost of maintaining the gut would be greater (Cant *et al.* 1996).

The key advantage of rapid digestion is the reduced feeding trip frequency, relative to slow digestion, that can be achieved in some foraging conditions. This reduction occurs under a wider range of modelled foraging conditions for the Common Murre than for the Herring Gull. This is because flight energy costs tend to be lower, and flight times shorter, for Herring Gulls, so that making extra trips in order to avoid the ingestion bottleneck is favoured, even in rapid digesters for which the bottleneck is less severe. Furthermore, in the Herring Gull, even when the slow digester does have to make more trips than the rapid digester, the cost is relatively small because flight is inexpensive in time and energy. A general conclusion can be drawn here: where flight costs per trip are small (whether the currency is time or energy), then the balance will tip towards slower digestion. Slow digesters can assimilate less energy per day, because their lower food processing rate is not fully compensated by their higher digestive efficiency. However, during a feeding period slow digestion actually gives the highest rate of assimilable energy gain, until the gut is filled (Figure 3.1). Therefore, in some circumstances slow digestion may allow the speediest return to the nest site carrying a given quantity of assimilable energy. Another outcome of the model is that high digestive efficiency does not necessarily correspond to high energetic efficiency (energy assimilated/energy expended in foraging, (Kacelnik 1984)). Since slow digesters frequently have to make more foraging trips per day than rapid digesters, and hence have greater flight energy expenditure, they are relatively inefficient foragers.

The model outcomes suggest that selection pressure on digestion strategy may differ according to foraging conditions, particularly for the Herring Gull. There may be

strong selection for plasticity of digestion strategy in this species. Indeed, it is noticeable that several of the traits which we suspect might have an influence on optimal digestion rates are not fixed within a species. Among seabird species, foraging range, diet and food acquisition rate vary greatly between colonies (Furness and Monaghan 1987). Given the plasticity of digestive traits in many animals (see Karasov 1996), it is possible that between-individual variation in gut retention time is partly explained by variations in feeding ecology.

It might be expected that pressure to reduce flight mass would result in selection for rapid digestion, particularly in Common Murres which have extremely high flight costs. However, in our model the birds nearly always make the return flight to the nest with a gut filled to capacity, so there is no mass difference between fast and slow digesters. It is not mass savings that favour rapid digestion, but rather the reduction of a food ingestion bottleneck. Only when the “sit-and-wait” strategy is used do significant energy savings arise because of mass loss through excretion.

ACKNOWLEDGEMENTS

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APPENDIX: CALCULATION OF FORAGING PARAMETER VALUES

1. Calculation of Energetic Costs

i) *Energy requirements of adults at the nest (E_{adult}):*

Common Murre: We assume that while not on a foraging trip the bird consumes energy at 2 x RMR. This allows for activities such as preening, interactions with partners or conspecifics, and chick feeding, which will increase energy expenditure above resting rate. Five published values of RMR were measured under similar conditions (Johnson and West 1975; Croll and McLaren 1993; Bryant and Furness 1995; Gabrielsen 1996; Gabrielsen *pers comm.*). Regression of these values on body mass yields the relationship $RMR \text{ (kJ/day)} = 0.007 \times \text{body mass (g)}^{1.9979}$ ($F_{1,3}=17.85$, $r^2=0.86$, $p=0.02$). For a Common Murre of mass 888 g this gives $RMR = 544 \text{ kJ/day}$, hence E_{adult} , the daily energy expenditure of an adult at the nest, is 1088 kJ/day.

Herring Gull: Published RMR values are 432 kJ/day and 415 kJ/day (Bennett and Harvey 1987; Bryant and Furness 1995), mean 424 kJ/day. As for the Common Murre we assume that E_{adult} is 2 x RMR, hence $E_{adult} = 848 \text{ kJ/day}$.

ii) *Energy requirements of the brood (E_{chick})*

Common Murre: We use the mean energy received by chicks in wild colonies = 286 kJ per chick per day (Harris and Wanless 1985 and references therein; Birkhead and Nettleship 1987; Harris and Wanless 1988).

Herring Gull: Data are available from captive chick rearing experiments (G. Hilton unpubl. data). At close to fledging mass, chicks were fed an average 1348.5 kJ/day, and were growing at a similar rate to healthy chicks in the colony. For a three-chick brood, this gives $E_{chick} = 4046 \text{ kJ/day}$.

iii) *Energy cost of feeding ($R_{feeding}$ and R_{water})*

Common Murre: Croll and McLaren (1993) measured energy expenditure during dive bouts as 15.3 W. However, their experiment was conducted in a warm (20°C) pool. De Leeuw (1996) showed that for each 1°C fall in water temperature, the metabolic cost of diving in Tufted Ducks, *Aythya fuligula*, increased by 0.23 W. Applying this effect to Common Murres gives an energy expenditure of 17.6 W at a water temperature of 10°C. In addition, De Leeuw (1996) demonstrated that

incorporating the energy costs of thermogenesis and dive-associated preening following a dive increases the overall energy expenditure by a factor of 2.8 above that measured simply within the dive-pause cycle in Tufted Ducks at 10°C. Therefore for Common Murres we set rate of energy expenditure during active feeding (R_{feeding}) as 50 W (= c. 2.8 x 17.6).

Croll and McLaren (1993) determined energy expenditure of Common Murres resting on water as 17.39 - (temperature (°C) x 0.6) W/kg. We use this to estimate rate of energy expenditure while resting on the water (R_{water}) as 12.8 W.

Herring Gull: Use a wider variety of feeding methods than Common Murres, but most of these involve relatively low cost activities, with rather little flying or diving (Verbeek 1977; Cramp and Simmons 1983; Pierotti and Annett 1987; Pons 1994). We therefore assume an R_{feeding} of 4.0 x RMR, = 19.6 W, and we estimate R_{water} as 2 x RMR = 10 W.

iv) *Energy cost of flight ($F(W)$)*

Program 1 (version 2) of Pennycuick's (1989) flight power calculation programs was used to estimate the power required for flapping flight in Watts (F), as a function of mass in g (W). We calculated the function $F(W)$ for flight at predicted minimum power velocity, which is very close to the observed flight speed of these species (Pennycuick 1987). Wingspan, wing area and aspect ratio data for the two species were taken from Pennycuick (1987); other parameter values were the default settings for the program.

2. Calculation of Foraging Parameters

i) *Foraging range (D) and flight speed (V)*

Common Murre: Foraging ranges during chick rearing have been estimated at many sites, and fall between 1.1 km and 110 km (see Bradstreet and Brown 1985; Phillips *et al.* in press for reviews). To estimate the time required to fly these distances we use a flight speed of 17.9 m/s (Pennycuick 1987)

Herring Gull: Foraging ranges during this period largely fall between 2 km and 30 km (Verbeek 1977; Pierotti and Annett 1991, Phillips *et al.* in press). We use a flight

speed of 11.3 m/s (Pennycuick 1987) to estimate flight time required to cover these foraging ranges.

ii) *Energy Density of Diet (Q)*

Common Murre: Predominantly piscivorous (Bradstreet and Brown 1985), and in general fish available as food to these birds fall within the range 4.0 - 8.0 kJ/g wet mass (Wallace and Hulme 1977; Harris and Hislop 1978; Montevecchi and Piatt 1984; Hislop *et al.* 1991), and Q is varied within this range.

Herring Gull: Eats a wider variety of foods, including items with much lower energy density e.g. earthworms, *Lumbricus spp.*, 2.97 kJ/g, shore crabs, *Carcinus spp.*, 3.35 kJ/g, starfish, *Asterias spp.*, 2.64 kJ/g (Hunt 1972), and Blue Mussels, *Mytilus edulis*, 1.8 kJ/g (Bustnes and Erikstad 1990; Kersten and Visser 1996), along with domestic refuse (7.8 kJ/g, Pons 1994) and fish. We allow Q to vary between 3 and 7 kJ/g wet mass for Herring Gulls.

iii) *Rate of Food Acquisition (S)*

Common Murres: Cairns *et al.* (1990) estimated that Common Murres in eastern Newfoundland eat 511 g of fish per day. They must also obtain c.18 g of food per day for the chick (Harris and Wanless 1985 and references therein; Birkhead and Nettleship 1987; Harris and Wanless 1988). Cairns *et al.* (1990) estimated that 117 minutes per day is spent diving. Given that 63 % of a foraging bout is spent underwater (Wanless *et al.* 1988), this gives a total foraging bout time of 186 minutes per day, hence $S_{\max} = 0.047$ g/sec.

Daily energy expenditure calculated from time budgets given in Monaghan *et al.* (1994) suggest daily energy expenditure of 1822 kJ and 1118 kJ in 1990 and 1991 respectively (using the activity-specific energy values used in this paper). At $TMEC_N$ of 0.79 (Hilton *et al.* submitted ms), and food energy density of 7.4 kJ/g (calculated from Hislop *et al.* (1991) for Sandlance, *Ammodytes spp.*, of the size eaten in Monaghan *et al.*'s (1994) study), this gives 312 g and 191 g eaten per day in 1990 and 1991 respectively, plus 18 g chick meals. Time spent in foraging bouts = 318 minutes and 89 minutes in 1990 and 1991 respectively, giving $S_{\max} = 0.016$ g/sec and $S_{\max} = 0.036$ g/sec for the two years. Averaging the results of these studies, we assume a value for S_{\max} of 0.037 g/sec.

Herring Gull: Rate of food acquisition appears to vary considerably between sites and food types (Verbeek 1977; Sibly and McLeery 1983; Pierotti and Annett 1987). Values appear to lie between c. 0.017 and 0.117 g/sec. We thus allowed S_{\max} to vary between 0.017 and 0.117 g/sec, but present results for an intermediate value of 0.067 g/sec.

3. Gut Capacity Constraints

Gut capacity of Common Murres and Herring Gulls was measured by dissection. The foregut (oesophagus and stomach) was excised, and digesta removed by flushing. The small intestine was clamped at the pylorus, and the foregut suspended from a clamp stand. We measured the volume of water that the foregut could hold. Capacity of the small and large intestine was measured by calculating volume from length and width measurements. We assume that digesta has a density of 1 g/ml. Total gut capacity of Common Murres and Herring Gulls was 192 ml (s.d. = 20.2) and 212 ml (s.d = 21.1) respectively. For the Herring Gull, which regurgitates food for the chick, there is an additional constraint: the chick meal can be no bigger than foregut capacity of 154 ml (s.d = 13.1). Common Murres carry (very small) chick meals in the bill.

LITERATURE CITED

- Afik, D. and Karasov, W.H. (1995) The trade-offs between digestion rate and efficiency in warblers and their ecological implications. *Ecology* **76**, 2247 - 57.
- Alexander, R.M. (1996) *Optima for animals*. Princeton University Press, Princeton, USA.
- Andersson, M. and Norberg, R.A. (1981) Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biol. J. Linn. Soc.* **15**, 105 - 30.
- Barton, N.W.H. and Houston, D.C. (1993a) A comparison of digestive efficiency in birds of prey. *Ibis* **135**, 363 - 71.
- Barton, N.W.H. and Houston, D.C. (1993b) The influence of gut morphology on digestion time in raptors. *Comp. Biochem. Physiol. A* **105**, 571 - 78.
- Barton, N.W.H. and Houston, D.C. (1994) Morphological adaptation of the digestive tract in relation to feeding ecology of raptors. *J. Zool. (Lond.)* **232**, 133 - 50.
- Baudinette, R.V. and Schmidt-Nielsen, K. (1974) Energy cost of gliding flight in Herring Gulls. *Nature* **248**, 83 - 4.
- Bennett, P.M. and Harvey, P.H. (1987) Active and resting metabolism in birds: allometry, phylogeny and ecology. *J. Zool. (Lond.)* **213**, 327 - 63.
- Birkhead, T.R. and Nettleship, D.N. (1987) Ecological relationships between Common Murres, *Uria aalge*, and Thick-billed Murres, *Uria lomvia*, at the Gannet Islands, Labrador. III. Feeding ecology of the young. *Can. J. Zool.* **65**, 1638 - 49.
- Bradstreet, M.S.W. and Brown, R.G.B. (1985) Feeding ecology of the Atlantic Alcidae. In *The Atlantic Alcidae: The evolution, distribution and biology of the Auks inhabiting the Atlantic Ocean and adjacent water areas* (Nettleship, D.N. and Birkhead, T.R. ed.s), pp.264-318. Academic Press, London, UK.
- Bryant, D.M. and Furness, R.W.(1995) Basal metabolic rates of north-atlantic seabirds. *Ibis* **137**, 219 - 26.
- Bukacinska, M., Bukacinski, D. and Spaans, A.L. (1996) Attendance and diet in relation to breeding success in Herring-Gulls (*Larus argentatus*). *Auk* **113**, 300 - 9.

- Burger, A.E. and Piatt, J.F. (1990) Flexible time budgets in Common Murres: Buffers against variable prey abundance. *Stud. Avian. Biol.* **14**, 71-83.
- Bustnes, J.O. and Erikstad, K.E. (1990) Size selection of Common Mussels, *Mytilus edulis*, by Common Eiders, *Somateria mollissima*, energy maximization or shell weight minimization. *Can. J. Zool.* **68**, 2280 - 3.
- Cairns, D.K., Bredin, K.A. and Montevecchi, W.A. (1987) Activity budgets and foraging ranges of breeding Common Murres. *Auk* **104**, 218 - 24.
- Cairns, D.K., Montevecchi, W.A., Birt-Friesen, V.L. and Macko S.A. (1990) Energy expenditures, activity budgets, and prey harvest of breeding Common Murres. *Stud. Avian. Biol.* **14**, 84 - 92.
- Calder, W.A., Calder, L.L. and Frazier, T.D. (1990) The hummingbird's restraint: a natural model for weight control. *Experientia* **46**, 999-1002.
- Cant, J.P., McBride, B.W. and Croom, W.J. (1996) The regulation of intestinal metabolism and its impact on whole animal energetics. *J. Anim. Sci.* **74**, 2541- 53.
- Castro, G., Stoyan, N. and Myers, J.P. (1989) Assimilation efficiency in birds: a function of taxon of food type ? *Comp. Biochem. Physiol. A* **92**, 271 - 8.
- Cramp, S. (1985) *Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic; Volume 4: Terns to Woodpeckers*. Oxford University Press, Oxford, UK.
- Cramp, S., and Simmons, K.E.L. (1983) *Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic; Volume 3: Waders to Gulls*. Oxford University Press, Oxford, UK.
- Croll, D.A. and McLaren, E. (1993) Diving metabolism and thermoregulation in Common and Thick-billed Murres. *J. Comp. Physiol. B* **163**, 160 - 6.
- Daan, S., Dijkstra, C. & Tinbergen, J.M. (1990) Family planning in the kestrel (*Falco tinnunculus*): the ultimate control of covariation of laying date and clutch size. *Behaviour* **114**, 83-116.

- De Leeuw, J.J. (1996) Diving costs as a component of daily energy budgets of aquatic birds and mammals - generalizing the inclusion of dive-recovery costs demonstrated in Tufted Ducks. *Can. J. Zool.* **74**, 2131 - 42.
- Demment, M.W. and Van Soest, P.J. (1985) A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *Am. Nat.* **125**, 641 - 72.
- Diamond, J.M., Karasov, W.H., Phan, D. and Carpenter, F.L. (1986) Digestive physiology is a determinant of foraging bout frequency in hummingbirds. *Nature* **320**, 62 - 3.
- Furness, R.W. and Monaghan, P. (1987) *Seabird Ecology*. Blackie, Glasgow, UK.
- Gabrielsen, G.W. (1996) Energy expenditure of breeding Common Murres. In *Studies of high-latitude seabirds. 4. Trophic relationships and energetics of endotherms in cold ocean systems* (Montevocchi, W.A. ed.), pp.49-58. Occasional Paper number 91, Canadian Wildlife Service, Ottawa, Canada.
- Guillemette, M. (1994) Digestive-rate constraint in wintering Common Eiders (*Somateria mollissima*) - implications for flying capabilities. *Auk* **111**, 900 - 9.
- Hammond, K.A. and Diamond, J. (1997) Maximal sustained energy budgets in humans and animals. *Nature* **386**, 457 - 62.
- Harris, M.P. and Birkhead, T.R. (1985) Breeding ecology of the Atlantic Alcidae. In *The Atlantic Alcidae: The evolution, distribution and biology of the Auks inhabiting the Atlantic Ocean and adjacent water areas* (Nettleship, D.N. and Birkhead, T.R. ed.s), pp.156-204. Academic Press, London, UK.
- Harris, M.P. and Hislop, J.R.G. (1978) The food of young Puffins *Fratercula arctica*. *J. Zool. (Lond.)* **185**, 213 - 36.
- Harris, M.P. and Wanless, S. (1985) Fish fed to young Guillemots, *Uria aalge*, and used in display on the Isle of May, Scotland. *J. Zool. (Lond.)* **207**, 441 - 58.
- Harris, M.P. and Wanless, S. (1988) The breeding biology of Guillemots *Uria aalge* on the Isle of May over a 6 year period. *Ibis* **130**, 172 - 92.
- Hatchwell, B.J. (1991) The feeding ecology of young Guillemots *Uria aalge* on the Skomer Island, Wales. *J. Anim. Ecol.* **133**, 153- 61.

- Hilton, G.M., Furness, R.W. and Houston, D.C. (submitted ms) A comparative study of digestion in North Atlantic seabirds. *J. Avian Biol.*
- Hilton, G.M., Houston, D.C. and Furness, R.W. (submitted ms) Which components of diet quality determine retention time of digesta in seabirds? *Funct. Ecol.*
- Hislop, J.R.G., Harris, M.P. and Smith, J.G.M. (1991) Variation in the calorific value and total energy content of the Lesser Sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. *J. Zool. (Lond.)* **224**, 501 - 17.
- Hunt, G.L.J. (1972) Influence of food distribution and human disturbance on the reproductive success of Herring Gulls. *Ecology* **53**, 1051 - 61.
- Jackson, S. (1992) Do seabird gut sizes and mean retention times reflect adaptation to diet and foraging method? *Physiol. Zool.* **65**, 674-697.
- Johnson, S.R., and West, G.C. (1975) Growth and development of heat regulation in nestlings and metabolism in adult Common Murre and Thick-billed Murre. *Ornis Scand.* **6**, 109 - 15.
- Kacelnik, A. (1984) Central place foraging in Starlings (*Sturnus vulgaris*). 1. Patch residence time. *J. Anim. Ecol.* **53**, 283-299.
- Karasov, W.H. (1990) Digestion in birds: chemical and physiological determinants and ecological implications. *Stud. Avian. Biol.* **13**, 391 - 415.
- Karasov, W.H. (1996) Digestive plasticity in avian energetics and feeding ecology. In *Avian Energetics* (Carey, C. ed.), pp.61-84. Chapman & Hall, New York, USA.
- Karasov, W.H. and Diamond, J.M. (1988) Interplay between physiology and ecology in digestion. *Bioscience* **38**, 602 - 11.
- Kenward, R.E. and Sibly, R.M. (1977) A Woodpigeon (*Columba palumbus*) feeding preference explained by a digestive bottleneck. *J. Appl. Ecol.* **14**, 815 - 26.
- Kersten, M. and Visser, W. (1996) The rate of food-processing in the Oystercatcher - food-intake and energy-expenditure constrained by a digestive bottleneck. *Funct. Ecol.* **10**, 440 - 48.
- Kirkwood, J.K. (1983) A limit to metabolizable energy-intake in mammals and birds. *Comp. Biochem. Physiol. A* **75**, 1 - 3.

- Levey, D.J. and Karasov, W.H. (1992) Digestive modulation in a seasonal frugivore, the American Robin (*Turdus migratorius*). *Am. J. Physiol.* **262**, G 711 - 18.
- Mateos, G.G., Sell, J.L. and Eastwood, J.A. (1982) Rate of food passage (transit-time) as influenced by level of supplemental fat. *Poult. Sci.* **61**, 94 - 100.
- Miller, M.R. and Reinecke, K.J. (1984) Proper expression of metabolizable energy in avian energetics. *Condor* **86**, 396 - 400.
- Monaghan, P., Walton, P., Wanless, S., Uttley, J.D. and Burns, M.D. (1994) Effects of prey abundance on the foraging behavior, diving efficiency and time allocation of breeding Guillemots *Uria aalge*. *Ibis* **136**, 214 - 22.
- Montevecchi, W.A. and Piatt, J. (1984) Composition and energy contents of mature inshore spawning Capelin (*Mallotus villosus*) - implications for seabird predators. *Comp. Biochem. Physiol. A* **78**, 15 - 20.
- Nelson J.B. (1988) Age and breeding in seabirds. In *Acta XIX Congressus Internationalis Ornithologici* (Ouellet, H. ed.), pp.1081- 97. University of Ottawa Press, Ottawa, Canada.
- Norstrom, R.J., Clark, T.P., Kearney, J.P. and Gilman, A.P. (1986) Herring Gull energy-requirements and body constituents in the great- lakes. *Ardea* **74**, 1 - 23.
- Pennycuick, C.J. (1987) Flight of auks (Alcidae) and other northern seabirds compared with southern Procellariiformes - ornithodolite observations. *J. Exp. Biol.* **128**, 335 - 47.
- Pennycuick, C.J. (1989) *Bird flight performance: A practical calculation manual*. Oxford University Press, Oxford, UK.
- Phillips R.A., Ratcliffe, N. and Riley H.T. (In Press) *Factors influencing the foraging range and marine distribution of UK seabirds with an evaluation of possible marine extensions to Special Protection Areas in Scotland*. Scottish Natural Heritage Research & Advisory Series, Scottish Natural Heritage, Edinburgh, UK.
- Pierotti, R. and Annett, C.A. (1987) Reproductive consequences of dietary specialisation and switching in an ecological generalist. In *Foraging Behaviour* (Kamil, A.C. ed.), pp.417 - 41. Plenum Publishing Corporation, New York, USA.

- Pierotti, R. and Annett, C.A. (1991) Diet choice in the Herring Gull - constraints imposed by reproductive and ecological factors. *Ecology* **72**, 319 - 28.
- Pons, J. (1994) Feeding strategies of male and female Herring Gulls during the breeding season under various feeding conditions. *Ethol. Ecol. Evol.* **6**, 1 - 12.
- Schoen, R.B. and Morris, R.D. (1983) Nest spacing, colony location and breeding success in Herring Gulls. *Wilson Bull.* **96**, 483 - 8.
- Sibly, R.M. (1981) Strategies of digestion and defaecation. In *Physiological Ecology: an evolutionary approach to resource use* (Townsend, C.R. and Calow, P. ed.s), pp. 109-139. Blackwell Scientific Publications, Oxford, UK.
- Sibly, R.M. and McLeery, R.H. (1983) Increase in weight of Herring-Gulls while feeding. *J. Anim. Ecol.* **52**, 35 - 50.
- Suarez, R.K. (1996) Upper limits to mass-specific metabolic rates. *Ann. Rev. Physiol.* **58**, 583 - 605.
- Verbeek, N.A.M. (1977) Comparative feeding ecology of Herring Gulls *Larus argentatus* and Lesser Black-backed Gulls *Larus fuscus*. *Ardea* **65**, 25 - 42.
- Wallace, P.D. and Hulme, T.J. (1977) *The fat/water relationship in the Mackerel Scomber scombrus L., Pilchard Sardina pilchardus (Walbaum), and Sprat Sprattus sprattus (L.), and the seasonal variation in fat content by size and maturity*. Fisheries Research Technical Report number 35. Ministry of Agriculture, Fisheries and Food, Directorate of Fisheries Research, Lowestoft, UK.
- Wanless, S., Harris, M.P. and Morris, J.A. (1988) The effect of radio transmitters on the behavior of Common Murres and Razorbills during chick rearing. *Condor* **90**, 816 - 823.
- Warner, A.C.I. (1981) Rate of passage of digesta through the gut of mammals and birds. *Nutr. Abs. Rev. B* **51**, 789 - 820.
- Weiner, J. (1989) Metabolic constraints to mammalian energy budgets. *Acta Theriol.* **34**, 3 - 35.
- Weiner, J. (1992) Physiological limits to sustainable energy budgets in birds and mammals - ecological implications. *TREE* **7**, 384 - 8.

Zwarts, L. and Dirksen, S. (1990) Digestive bottleneck limits the increase in food-intake of Whimbrels preparing for spring migration from the Banc-d'Arguin, Mauritania. *Ardea* **78**, 257 - 78.

chapter 4

THE EFFECT OF DIET QUALITY, SWITCHING DIETS, AND MIXING DIETS ON DIGESTION PARAMETERS OF SEABIRDS

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Hilton. G.M., R.W. Furness and D.C. Houston. The effect of diet quality, switching diets, and mixing diets on digestion parameters of seabirds.

ABSTRACT

Because animals modulate the function of their digestive system in order to optimise digestion of the diet they are currently eating, changing the type of food eaten might result in temporarily reduced digestive performance. Species which typically do not change diet frequently are expected to be less able to adjust their digestive function to cope with diet changes than species which frequently switch between food types. We tested these predictions for two contrasting seabird species - a specialist piscivore, the Common Guillemot (*Uria aalge*), and the opportunistically feeding Lesser Black-backed Gull (*Larus fuscus*) - fed on two fish diets. Birds were acclimated to one of the diets, and then abruptly switched to the other. Following the diet switches, birds showed large changes in retention time of digesta. When Whiting (*Merlangius merlangus*) acclimated Common Guillemots were switched to a Sprat (*Sprattus sprattus*) diet, some birds showed very large declines in digestive efficiency. Common Guillemots also showed a reduction in digestive efficiency when given both diets in a mixed meal. Common Guillemots appear to have a less flexible and efficient digestive system than Lesser Black-backed Gulls. We suggest that this difference in response of the two species is related to their differing feeding ecology.

ABBREVIATIONS: EEL_N Nitrogen-corrected endogenous energy losses · $E_{(Sprat)}$, $E_{(Whiting)}$ energy consumed in Sprat and Whiting respectively · GE_i , GE_o energy density of food and excreta respectively · m_i dry mass of excreta produced in the i th time interval since feeding · N_c Nitrogen correction factor · N_i , N_o percent Nitrogen content of food and excreta respectively · Q_i , Q_o dry mass of food ingested and excreted respectively · $TMEC_N$ Nitrogen-corrected true metabolisable energy coefficient · $TME_{N(predicated)}$ predicted Nitrogen-corrected true metabolised energy · t_i time (hours) since feeding.

INTRODUCTION

Animals alter digestive processes in response to changes in the characteristics of the diet (Karasov 1996). For example, changes in mass of stomach musculature, small intestine and caeca length, digestive enzyme levels, and nutrient transport activity have all been recorded after changes of diet (e.g. Miller 1975; Karasov 1992; Piersma et al. 1993; Martinez del Rio et al. 1995; Piersma and Lindstrom 1997). These changes are assumed to allow animals to optimise their digestive performance (Sibly 1981; Penry and Jumars 1987; Karasov 1996).

Presumably an animal cannot achieve its maximum performance on more than one diet simultaneously. Plasticity of digestive function allows an animal to improve its performance on its current diet, but this process may mean that digestive performance is reduced if a different food is eaten (Levey and Karasov 1989). Thus one might predict that if animals are acclimated to one particular diet, and are then switched to a novel diet, their digestive performance will initially be reduced, in comparison with animals acclimated to the novel diet. Furthermore, one might expect that if an animal eats more than one food type simultaneously then its digestive performance will be less good than if it ate the same food types exclusively and separately. Thus an animal may benefit from adapting its gut function to its current diet, because its digestive performance improves, but it may pay a cost if it subsequently eats a different diet.

Previous diet switching experiments have shown that digestive performance does suffer when switches onto novel diets are made (Levey and Karasov 1989; Lodge 1994; Afik and Karasov 1995). However, all such studies have involved extreme changes in the nature of the diet. In this study we measured digestive function of seabirds acclimated to one of two species of marine fish which are commonly eaten by seabirds. The diets differed in lipid content, and therefore energy density, but little else. We then investigated the costs incurred when the diet was abruptly switched to the other fish. Finally, we measured digestive function of birds given mixed meals of both fish species, and compared this with their performance when eating the two diets separately, to test for a cost of mixing food types.

One would expect that animals which are generalist feeders, regularly changing between food types, would be adapted for rapid modification of their digestive function in response to diet changes (Lee and Houston 1993), because this would reduce the cost of changing diet. However, in specialist feeding animals, which eat a very narrow range of food types, such an ability might be less important. We therefore selected two seabird species for these experiments which are of similar body mass, but which differ in the breadth of their dietary niche: Common Guillemots are specialist piscivores, eating almost entirely small shoaling fish, and tending above all to select lipid-rich species. At any given breeding site the range of fish species selected tends to be very small (Bradstreet and Brown 1985). Lesser Black-backed Gulls are primarily piscivorous, but also eat invertebrates, refuse, birds and carrion (Cramp and Simmons 1983). These latter food items tend to be lower in energy density, and more resistant to digestion than fish (Hunt 1972; Jackson et al. 1987; Pons 1994). We tested the hypothesis that any costs incurred when the birds were given dietary “challenges” (switching diets and mixing diets) would be greater for the Common Guillemot than for the Lesser Black-backed Gull.

Our assessment of digestive performance was based on measurement of two fundamental gut function parameters: retention time of digesta, and digestive efficiency. Digestive efficiency (which we measured as Nitrogen-corrected True Metabolisable Energy Coefficient, $TMEC_N$) determines the quantity of a food that has to be eaten in order to assimilate a given amount of energy. Retention time is important because a causal trade-off between retention time and digestive efficiency is expected (Afik and Karasov 1995). In addition, the rate at which food is evacuated from the gut determines the maximum rate at which food can be ingested (Kenward and Sibly 1977; Kersten and Visser 1996). Furthermore, the reduction in mass resulting from rapid excretion of undigested food can bring energy savings through reduced costs of locomotion (Sibly 1981), and can also potentially improve foraging ability (Barton and Houston 1993a; 1994).

METHODS

Experimental diets

We selected two fish species: Sprat, which has a high energy density due to its high lipid content; and Whiting, which has a comparatively low energy density (Hislop et al. 1991). Samples were caught in the southern North Sea during March 1996, stored at -20°C, and thawed immediately prior to feeding. They were moistened and fed at 5 - 10°C.

We determined the relationship between wet mass and energy/Nitrogen content of the two diets, in order to estimate energy and Nitrogen input in the experimental meals. Fish were thawed and weighed, dried at 55°C in a fan-assisted oven, and homogenised in a liquid-Nitrogen freezer mill. Fractions of the homogenate were then used to determine percentage Nitrogen, using a Leco FP-328 Elemental Nitrogen Analyser, and energy content, using a Parr Adiabatic Bomb Calorimeter.

Wet mass of each fish (± 0.1 g) used in the feeding trials was recorded. The following relationships were used to calculate energy and Nitrogen content of each fish fed in the experiments:

Sprat:

energy content (kJ) = $3.234 \times \text{wet mass (g)}^{1.345}$; $F_{1,29} = 689.3$; $r^2 = 0.96$; $p < 0.0001$.

Nitrogen content (g) = $0.0477 \times \text{wet mass (g)}^{0.756}$; $F_{1,10} = 10.4$; $r^2 = 0.67$, $p = 0.009$.

Whiting:

energy content (kJ) = $3.737 \times \text{wet mass (g)}^{1.046}$; $F_{1,23} = 1758$; $r^2 = 0.99$, $p < 0.0001$.

Nitrogen content (g) = $0.0228 \times \text{wet mass (g)}^{1.037}$; $F_{1,23} = 6691$; $r^2 = 1.00$, $p < 0.0001$.

Nutrient composition of the diets was also determined (Table 4.1). Lipid extraction was performed in a soxhlet analyser, with chloroform as solvent. Crude protein content was calculated as percent nitrogen $\times 6.25$ (Crisp 1971). Ash content was determined by combusting lipid-free samples at 650°C in a muffle furnace for 12 hours. Sprat had over five times the lipid content of Whiting, and correspondingly lower water content. The diets differed very little in other respects.

Table 4.1: Summary of the chemical composition of the Sprat and Whiting diets.

	Sprat		Whiting	
	Common Guillemot	Lesser Black- backed Gull	Common Guillemot	Lesser Black- backed Gull
energy kJ g ⁻¹	7.84±0.55	7.93±0.57	4.28±0.04	4.43±0.05
crude protein (%)	15.98±0.78	15.85±0.80	15.90±0.11	16.33±0.14
lipid (%)	11.01±1.86	11.33±2.00	1.92±0.05	1.73±0.06
ash (%)	3.96±0.16	3.98±0.16	3.37±0.11	3.83±0.15
water (%)	69.97±1.15	69.77±1.18	77.44±0.07	77.72±0.09

Values are expressed on a wet mass basis as means ± s.d.. For each component, a power regression with wet mass (g) as independent variable and mass of component (g) as dependent variable was calculated, and values were calculated from wet mass of individual fish fed to each bird species - diet combination.

Feeding trial protocol

Digestion trials were carried out in 1996 on recently fledged Lesser Black-backed Gulls, at Walney Island, Cumbria, and in 1997 on non-breeding adult Common Guillemots at Hornøy, Finnmark, northern Norway. Before the digestion trials, birds were maintained in groups for a three-week acclimation period, during which time half of them were fed solely on Sprat, and the other half on Whiting. Birds were fed three times daily on a ration sufficient to allow the completion of normal growth for the Lesser Black-backed Gulls, and body mass maintenance for the Common Guillemots. Birds learnt to feed themselves within one - four days of being taken into captivity.

Following the acclimation period, birds were placed in individual, 55 cm diameter, open - topped plastic cages for digestion trials. The cages had a 1.5 cm galvanised

weldmesh floor supported above removable plastic excreta collecting trays (60 cm x 60 cm).

Birds were weighed and then caged on the afternoon prior to the start of the digestion trial, and fed in the cages at 2000 hrs with a meal of similar size to the trial meals. Birds were fed two trial meals per day, at 0800 hrs - 0845 hrs, and at 2000 hrs - 2045 hrs. Most birds in the 1996 experiment ate the meals voluntarily, and those that did not were fed by hand. In 1997 all birds were fed by hand. The meal sizes were sufficient to allow the birds to maintain body mass. Table 4.3 shows details of food consumption during the experiments. Whiting meals tended to be heavier than Sprat meals, because less Sprat was needed for mass maintenance. Note that Common Guillemots were fed considerably smaller Whiting than were the Lesser Black-backed Gulls. This was because Common Guillemots reject larger fish (Swennen and Duiven 1977), whereas gulls are adapted to eating very large food items.

The experimental design follows that used by Lodge (1994), who switched European Starlings from good to poor diets, and vice-versa. The trials lasted for six days. Digestion parameters ($TMEC_N$, and mean retention time) were measured on days one, two, three and six. On days four and five birds were returned to the pens, but remained on the experimental diets.

On day one of the cage trials all birds were fed on their acclimation diet, to obtain a baseline set of digestion parameters. In 1996, on day two half of the birds were then switched to the alternative diet for five days, whilst the remaining birds remained on the acclimation diet. The latter birds, whose diet had not changed, acted as controls to determine whether changes in digestion parameters were due to diet switching, or were due to being kept in cages. In fact neither of the digestion parameters changed in either the Sprat- or the Whiting-fed control groups during the course of the trial (repeated measures ANOVA using values for days one - six, $F_{3,15} < 1.5$ for all groups; n.s.). Therefore, because of the practical difficulties of keeping large numbers of birds in captivity, we did not use non-switched birds as controls in 1997. Instead, the control values for 1997 were those obtained on day one of the trial when birds were still eating their acclimation diet. We therefore assumed that changes in digestion parameters after the diet switches were due to the diet effect, and not to cage-effects.

We are confident that this assumption is valid, because the changes we observed in digestion parameters were in opposite directions for the birds switched from Sprat to Whiting than for birds switched from Whiting to Sprat.

We made two types of comparison to test for effects of diet switches on digestion parameters. T-tests were used to compare digestion parameters of birds which had been switched onto a novel diet with the values obtained for the same diet from acclimated birds. We used repeated measures ANOVA to test for changes in retention time and digestive efficiency of switched birds over the course of the experiment. Where there were significant changes in digestion parameters, paired t-tests were used to test for changes in digestion parameters between consecutive trial days. Values of $TMEC_N$ were arcsine transformed for statistical analyses.

To determine the effect of diet mixing on $TMEC_N$ we gave separate groups of birds meals consisting of approximately equal proportions (by energy content) of Whiting and Sprat. All other experimental procedures were identical to the main diet switching experiments. Prior to the diet mixing experiment we measured the $TMEC_N$ of each individual bird on Whiting and on Sprat, on successive days. For each bird we calculated its predicted value of digestive efficiency on the mixed diet, from the values obtained for that bird on each of the diets separately; we compared this predicted value with the observed value (see below).

In order to examine whether there were measurable changes in digestive function during acclimation, we compared digestion parameters of Common Guillemots before and after the three week period. Twelve non-breeding birds were captured and immediately placed in the experimental cages. Half of the birds were fed on Sprat, and half on Whiting, in two-day digestion trials identical to those used in the main experiment. The digestion parameters of these birds were compared with those obtained from birds on the same diets at the end of the acclimation period.

Calculation of $TMEC_N$ and mean retention time

Energy And Nitrogen Determinations

Excreta trays were removed at one, three, five, seven, nine and twelve hours after the morning meal. All excreta were placed into vials, and frozen at -20°C . Samples were subsequently thawed, dried at 55°C in a fan-assisted oven, and homogenised in an electric grinder. Percent Nitrogen content and energy content were determined as for fish samples.

Digestive Efficiency

In calculating Nitrogen-corrected True Metabolisable Energy Coefficients ($TMEC_N$) for our birds we followed the methodologies proposed by Sibbald (1976), Miller and Reinecke (1984) and Wolynetz and Sibbald (1984).

Nitrogen-corrected endogenous energy losses (EEL_N , kJ per kg body mass per day) were estimated for separate groups of Common Guillemots ($n = 10$) and Lesser Black-backed Gulls ($n = 6$), fed on Sprat and Whiting respectively, using the same procedures as in the main experiment. Each bird was used for two or three determinations (on successive days). Gross energy ingested per day varied between 368 and 1815 kJ. We regressed N-corrected energy excreted per kg body mass (kJ) on gross energy ingested (kJ). The y-intercept of the linear regression was taken as EEL_N .

In ANCOVA, neither slope nor elevation of the regression differed between Common Guillemots and Lesser Black-backed Gulls ($F_{1,39} = 1.95$, n.s. and $F_{1,40} = 2.66$, n.s. respectively). Therefore for both study species we defined EEL_N per day as the intercept of the common linear regression:

$$y = 0.268 x + 47.5; F_{1,41} = 210, p < 0.0001, r^2 = 0.83.$$

Hence we estimated EEL_N as $47.5 \text{ kJ kg d}^{-1}$.

We also corrected Metabolised Energy estimates to zero Nitrogen retention by calculating a Nitrogen Correction Factor (N_c):

$$N_c = \left((Q_i \cdot N_i) - (Q_o \cdot N_o) \right) \cdot 34.4 \text{ kJ g}^{-1}$$

where Q_i = dry mass of food ingested (g), Q_o = dry mass of excreta (g), N_i = percent Nitrogen content of food, N_o = percent Nitrogen content of excreta, and 34.4 kJ g^{-1} = estimated energy density of excretory Nitrogen (Harris 1966).

TMEC_N was calculated as:

$$\frac{(Q_i \cdot GE_i) - (Q_o \cdot GE_o - EEL_N) + N_c}{Q_i \cdot GE_i}$$

where GE_i = energy density ($\text{kJ g dry mass}^{-1}$) of food, and GE_o = energy density ($\text{kJ g dry mass}^{-1}$) of excreta. We express TMEC_N as a percentage.

In the mixed diet experiment, predicted TMEC_N was calculated as:

$$\text{TME}_{N(\text{predicted})} = (E_{(\text{Whiting})} \times \text{TMEC}_{N(\text{Whiting})}) + (E_{(\text{Sprat})} \times \text{TMEC}_{N(\text{Sprat})})$$

where $\text{TME}_{N(\text{predicted})}$ is predicted True Metabolised Energy (TME_N), $E_{(\text{fish type})}$ is the energy ingested in that fish type (kJ), and $\text{TMEC}_{N(\text{fish type})}$ is observed TMEC_N on that fish type on previous days. Predicted TMEC_N was then calculated as:

$$\frac{Q_i \cdot GE_i - \text{TME}_{N(\text{predicted})}}{Q_i \cdot GE_i}, \text{ and expressed as a percentage.}$$

Retention time

Retention time of digesta was calculated from timed faecal collections during the twelve hours following the first meal of the day. Earlier trials indicated that excretion of a meal was complete, or almost so, within this 12 hour period. Mean 12 hour retention time of digesta was calculated as:

$$\text{mean retention time} = \sum_{i=1}^n m_i \cdot t_i / \sum_{i=1}^n m_i$$

where m_i is the amount of excreta produced in the i th time interval (g dry mass), and t_i is the time (hours) since the trial meal (Blaxter et al. 1956).

Do juvenile gulls have similar digestive tracts to adults ?

Juvenile Lesser Black-backed Gulls were used in the feeding trials because they were easier to tame than adults. To test whether the young gulls we used were adequate models of adult gulls, we compared the gross gut morphology of adult and fledgling gulls. We dissected birds from the study colony which had died in collisions, and

measured proventriculus, ventriculus and small intestine dimensions, and skeletal morphometrics. Excised tissues were wrapped and frozen at -20°C. After two months of storage, tissues were dried at 55°C in a fan-assisted oven, and weighed (± 0.001 g).

To control for body size in comparisons of digestive tract size we calculated a skeletal body size measure. We performed a principal components analysis on the correlation matrix of skull length, ulna length, femur length and keel length. The first principal component axis was taken as a measure of skeletal body size (Rising and Somers 1989). There was no significant difference between adults and fledgling gulls in skeletal body size (Table 4.2). We therefore used t-tests to compare gut morphology parameters of adults and fledglings. Table 4.2 shows that there were no significant differences between adults and fledglings in any gut morphology parameter. It therefore seems reasonable to assume that fledglings serve as a good model for digestive function in adult gulls.

Table 4.2: Comparison of gross gut morphology of adult and recently fledged Lesser Black-backed Gulls.

	adult (n=32)	recently fledged (n=16)
body mass (g)	799 \pm 17	823 \pm 33
skeletal body size	0.21 \pm 0.14	0.31 \pm 0.18
proventriculus mass (g)	0.83 \pm 0.03	0.79 \pm 0.04
ventriculus mass (g)	4.23 \pm 0.21	4.47 \pm 0.15
small intestine mass (g)	3.25 \pm 0.18	3.31 \pm 0.21
stomach surface area (cm ²)	3.92 \pm 0.14	4.33 \pm 0.25
small intestine surface area (cm ²)	18.20 \pm 0.97	20.75 \pm 1.52
small intestine length (mm)	978 \pm 23	1021 \pm 39

Values are means \pm s.d.. No significant differences between adults and fledglings for any parameters (t-tests n.s.).

RESULTS

Changes in body mass over the course of the experiments were trivial (Table 4.3), so the birds were probably close to zero energy balance. For both diets, meal masss differed little between bird species. Energy density of Sprat was approximately 80% higher than that of Whiting (Table 4.1).

Table 4.3: Meal mass, fish mass and bird mass during digestion trials.

	Common Guillemot	Lesser Black-backed Gull
mean body mass (g)	934±68	759±90
mean daily mass change (%)	+0.000	-0.008
mean daily intake of Sprat (g)	177±7.20	157±8.3
mean Sprat meal energy (kJ)	1404±83	1265±81.3
mean mass of individual Sprats (g)	13.2±2.69	13.7±2.9
mean daily intake of Whiting (g)	207±6.11	212±39.3
mean Whiting meal energy (kJ)	886±28	939±174
mean mass of individual Whiting (g)	19.6±3.82	41.0±9.36

Values are means ± s.d..

Digestion parameters of Birds after the acclimation period

For Common Guillemot, retention time of Sprat was significantly shorter than retention time of Whiting, but paradoxically, the reverse was true for Lesser Black-backed Gull. If we compare how the two bird species handled the same diet, Common Guillemots showed significantly shorter retention time of Sprat than Lesser Black-backed Gulls, but on the Whiting diet there was no significant retention time difference between the species (Table 4.4).

Table 4.4: Control (day one) digestion parameters of Sprat and Whiting fed to Common Guillemots and Lesser Black-backed Gulls.

	Diet		
	Sprat	Whiting	t-test (diet effect)
Gut Retention Time ¹			
Common Guillemot	4.85 ±0.11 (6)	5.29 ±0.16 (5)	p<0.05
Lesser Black-backed Gull	5.52 ±0.12 (12)	5.10 ±0.14 (12)	p<0.01
t-test (species effect)	p<0.01	n.s.	
Digestive Efficiency ²			
Common Guillemot	79.78 ±0.72 (6)	74.52 ±0.35 (5)	p<0.01
Lesser Black-backed Gull	82.66 ±0.69 (12)	73.40 ±0.46 (12)	p<0.001
t-test (species effect)	p<0.05	n.s.	

¹: Values are mean ± 1 s.e.m. 12 hour retention time (hours), with sample size.

²: Values are mean ± 1 s.e.m. percent TMEC_N, with sample size.

For both species TMEC_N (hereafter referred to as digestive efficiency) was considerably higher in Sprat-fed birds than Whiting-fed birds (Table 4.4). Digestive efficiency of Common Guillemots fed Sprats was significantly lower than that of Lesser Black-backed Gulls, but there was no significant difference between the species on the Whiting diet. The between-species comparison for the Whiting diet is probably misleading however, because the Whiting fed to the Common Guillemots were much smaller than those fed to the gulls, and hence may have been easier to digest.

Effect of diet switches

Both diet-switched groups in both species showed significant changes in retention time and digestive efficiency over the course of the six day experiment (Repeated measures ANOVA, $F_{3,15} > 4.15$, $p < 0.05$), except for the Sprat to Whiting Common Guillemot group, which showed no significant changes in retention time ($F_{3,15} = 2.14$, n.s.).

Retention Time

When Whiting-acclimated Common Guillemots were switched to Sprat, their retention times immediately decreased (paired t-test, $t_4 = 3.44$; $p = 0.026$); this decrease continued on day three (paired t-test, $t_4 = 5.28$; $p = 0.006$), such that the switched birds had shorter retention time than control birds, by 21 minutes (t-test, $t_9 = 2.48$; $p = 0.035$). This difference persisted on day 6 (Figure 4.1a) (t-test, $t_9 = 2.50$; $p = 0.034$). The excreta of some of the birds became diarrhoeic following the switch, and it appeared that the reduction in retention time involved a physiological malfunction.

By contrast, when Whiting-acclimated Lesser Black-backed Gulls birds were switched to Sprat, their retention times immediately increased, up to the level of control Sprat-acclimated birds (paired t-test, day two > day 1; $t_5 = 4.09$; $p = 0.009$). For the remainder of the experiment there were no further changes in the retention times of the diet-switched group (Figure 4.1a).

When switched to Whiting, Sprat-acclimated Lesser Black-backed Gulls showed a significant reduction in retention time between day two and day three (paired t-test, $t_5 = 2.57$; $p = 0.05$), which brought them to a similar level to that of the control birds. However, between days three and six there was a significant increase in retention time of the switched birds (paired t-test, $t_5 = 3.47$; $p = 0.04$). On day six the switched birds had a retention time of Whiting that was significantly (47 minutes) greater than that of control Whiting-acclimated birds (t-test, $t_{16} = 3.25$; $p = 0.005$) (Figure 4.1b).

When Sprat-acclimated Common Guillemots were switched to Whiting they showed an immediate (but non-significant) increase in retention time that brought them to a level close to that of control birds, and thereafter there were no further changes in retention time of the switched birds (Figure 4.1b).

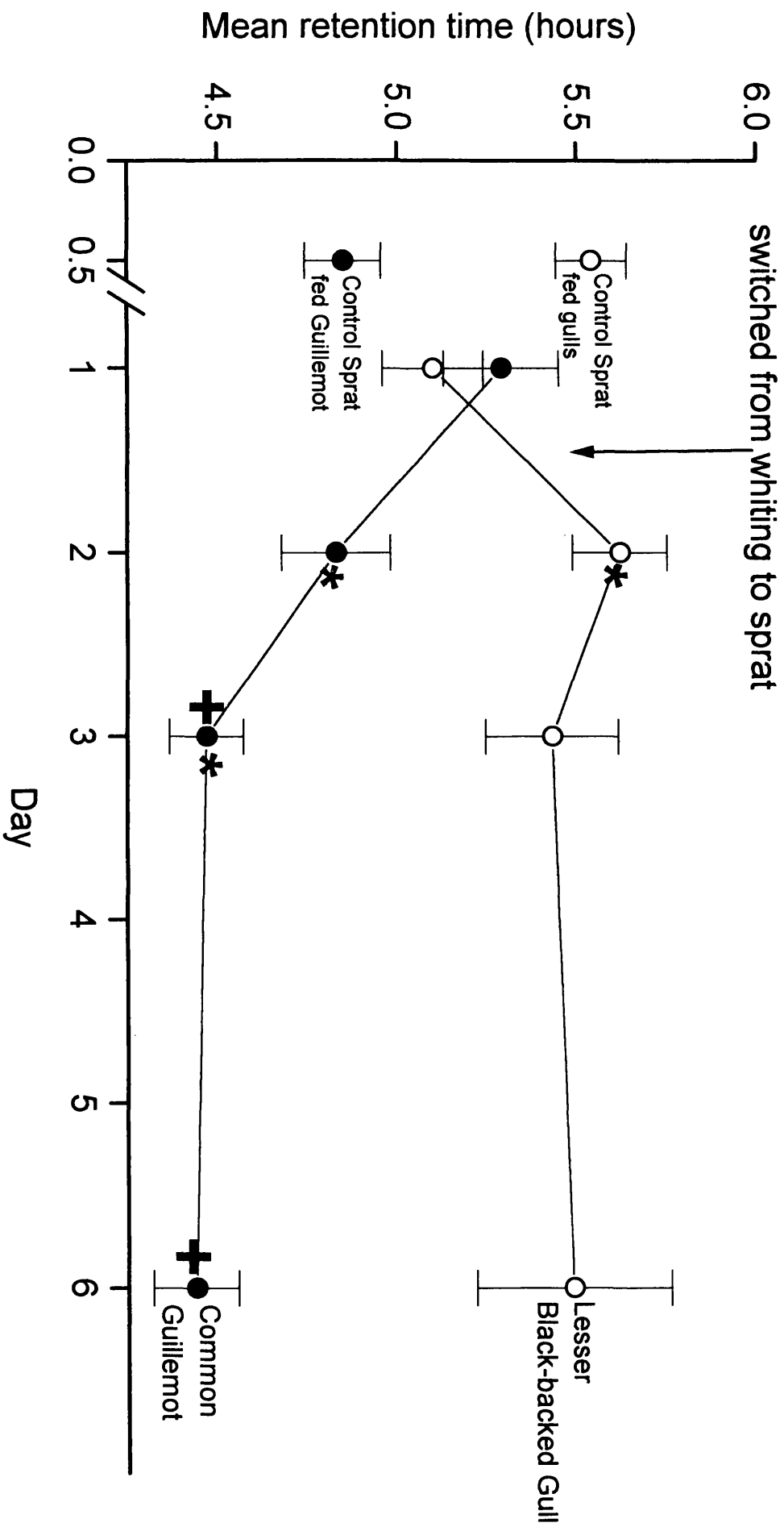
Fig 4.1: Changes in mean retention time of digesta following diet switches.

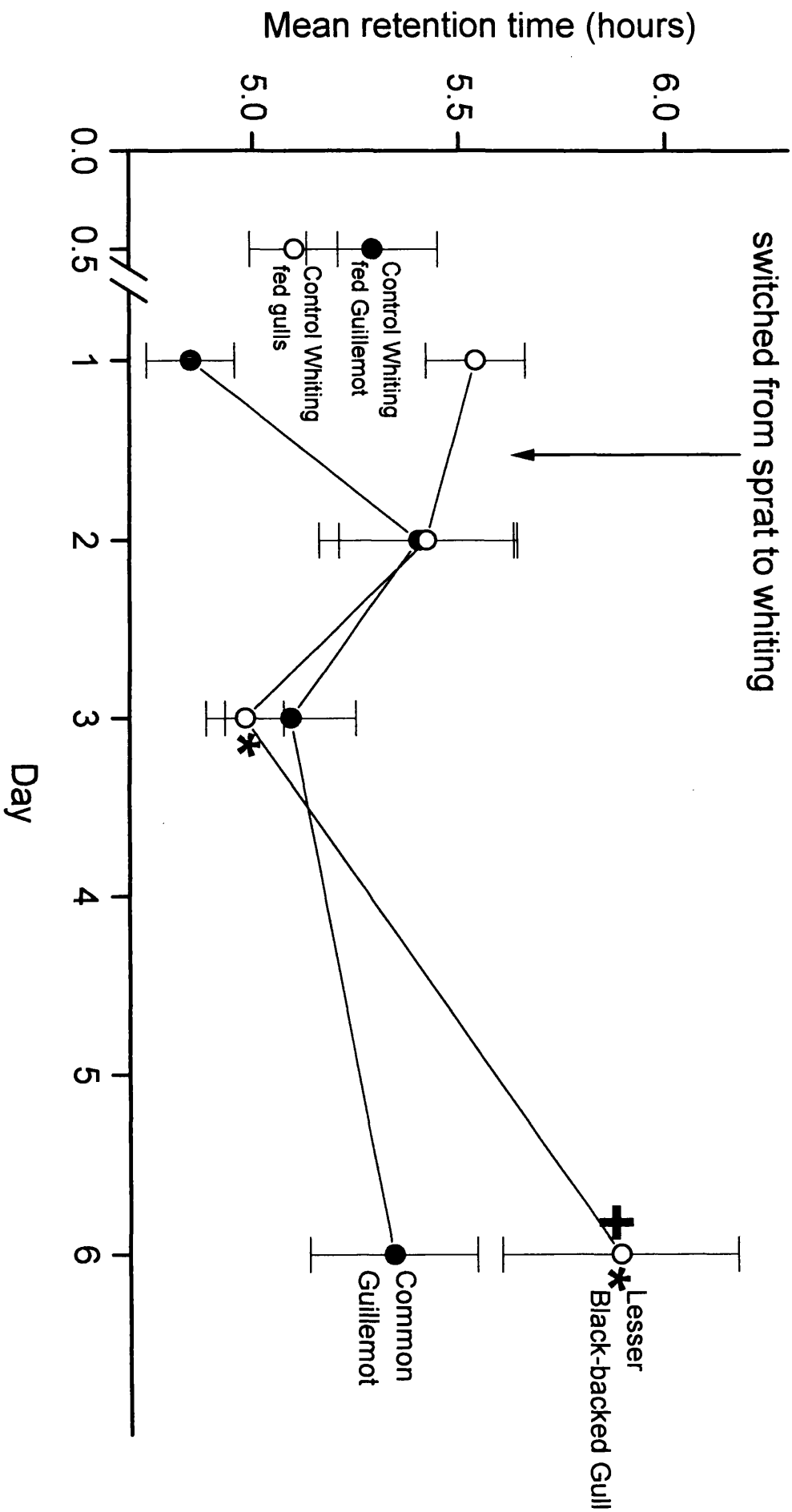
(a) following Whiting to Sprat switches.

(b) following Sprat to Whiting switches.

Open circles: Lesser Black-backed Gulls (n=6); closed circles Common Guillemots (n=5 for Whiting to Sprat switch, n=6 for Sprat to Whiting switch). Plotted values are means \pm 1 s.e.m.. Control values are shown for comparison using the same species symbols; they represent values for acclimated birds on the diet which birds were switched onto. Values plotted for day one are those obtained prior to the switch.

*: values differ significantly from the previous day (repeated measures ANOVA with paired t-test, $p < 0.05$). +: values differ significantly from control values (t-tests).





Digestive Efficiency

Control digestive efficiency values differed considerably between diets (Table 4.4); however, on switching to novel diets, birds immediately showed shifts in digestive efficiency such that they did not differ from control values for the new diet (Figure 4.2a; Figure 4.2b).

However, over days two - six, both switch groups of Lesser Black-backed Gulls showed significant increases in digestive efficiency of 2.0 - 2.5% (Sprat to Whiting switch, paired t-test, day six > day three, $t_5=3.37$; $p=0.020$; Whiting to Sprat switch, paired t-test, day three > day two, $t_5 = 7.07$; $p=0.001$). Indeed, the Whiting to Sprat switch group had a significantly higher digestive efficiency, by 1.7%, than control birds on days three and six (t-test, $t_{16} = 2.24$; $p=0.04$ for both comparisons). Common Guillemots switched from Sprat to Whiting showed no improvement in digestive efficiency over the five days following the switch (Figure 4.2b). Furthermore, the Whiting to Sprat switch group actually showed a progressive reduction of 4.6% in digestive efficiency over days two - six (Figure 4.2a). This reduction in efficiency was not significant, because the response differed between individuals, and because variance in digestive efficiency was very large on day six. The lowest control value of digestive efficiency for Common Guillemots on a Sprat diet was 77.1% ($n=6$ birds), whereas four out of the five switch birds had digestive efficiency below 77% on day six. One bird suffered a massive reduction in digestive efficiency, to 61.9%, but apart from inefficient and diarrhoeic digestive function, the bird was otherwise healthy.

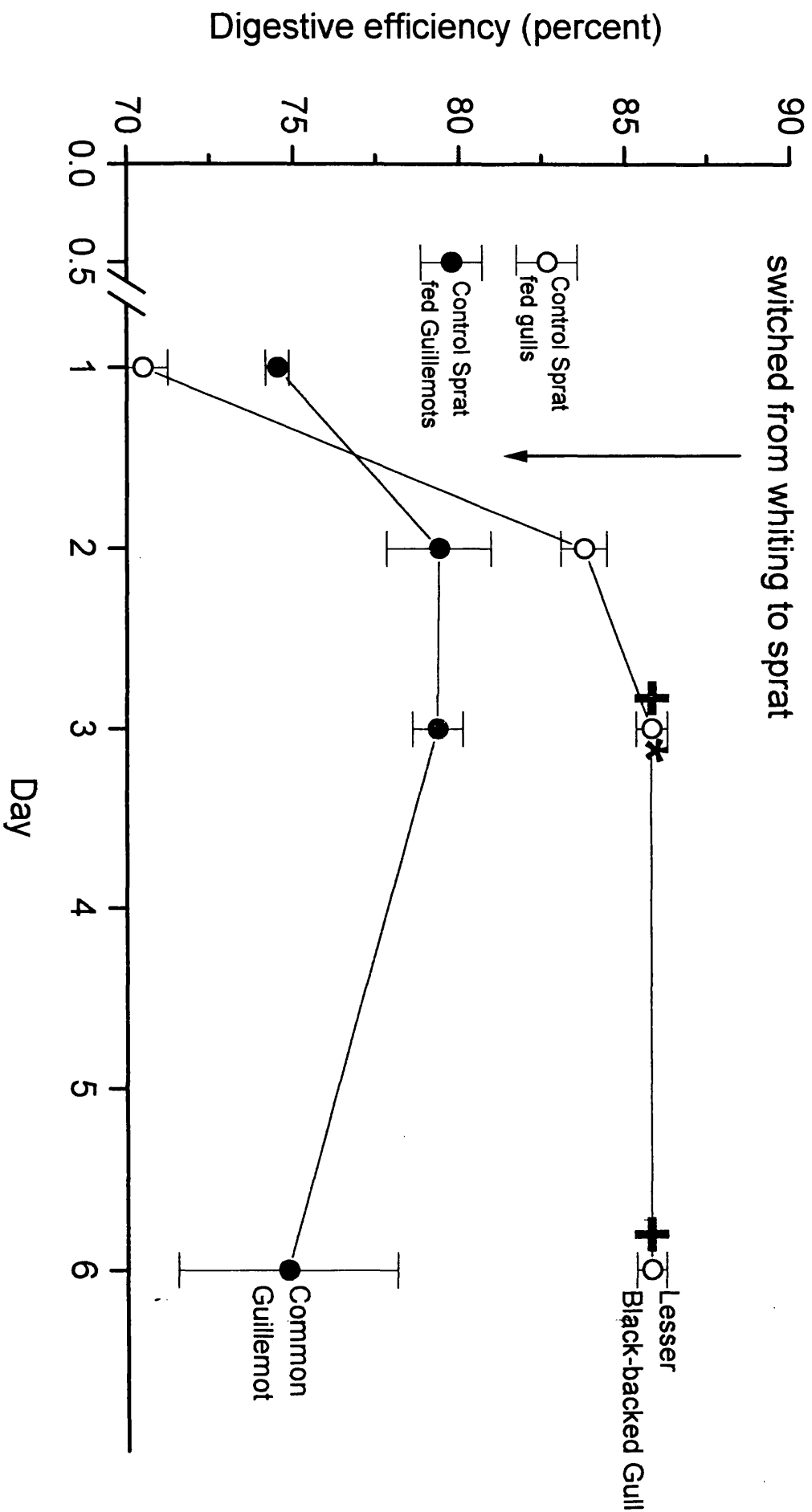
Fig 4.2: Changes in digestive efficiency (TMEC_N) following diet switches.

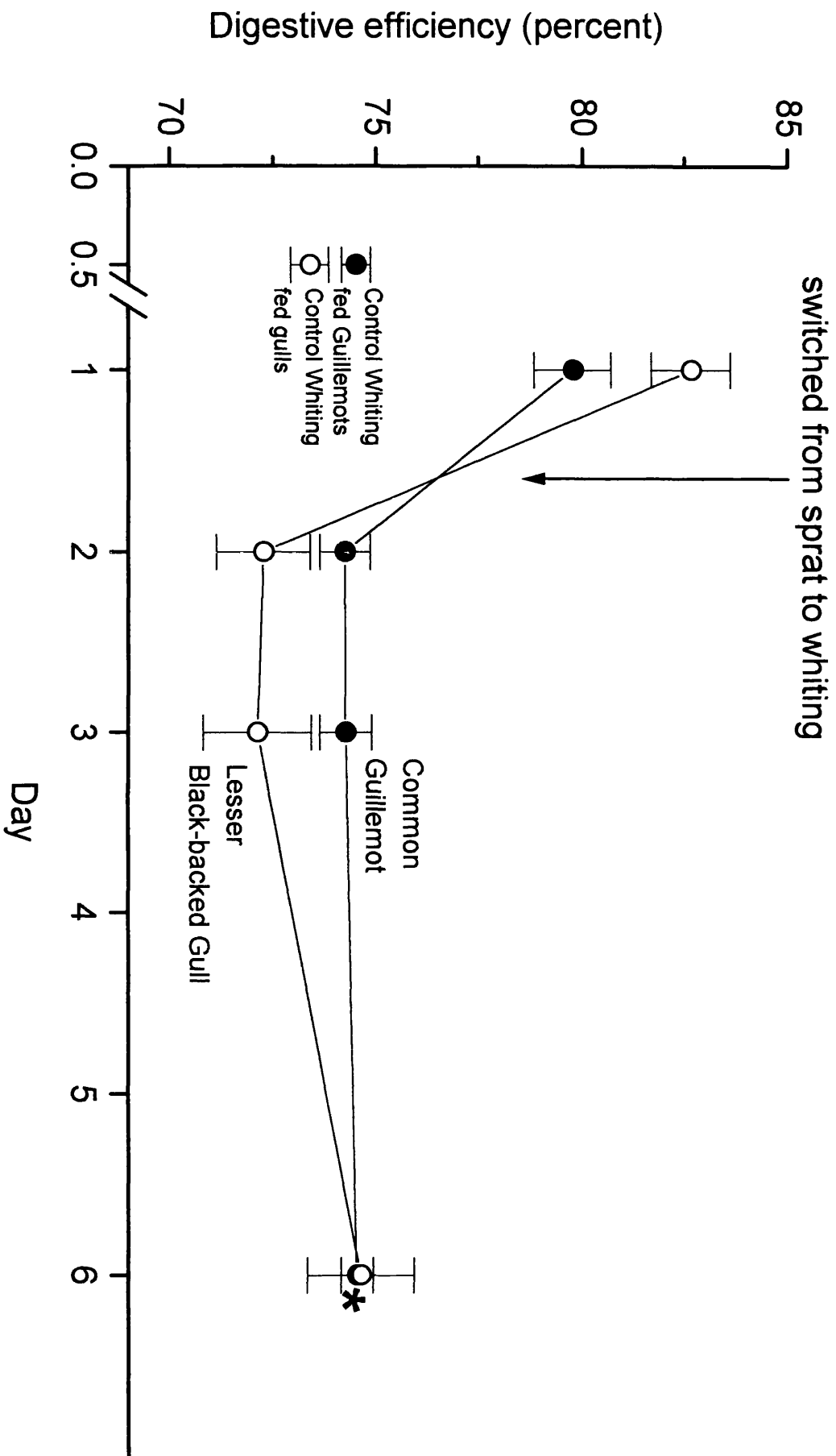
(a) following Whiting to Sprat switches.

(b) following Sprat to Whiting switches.

Open circles: Lesser Black-backed Gulls (n=6); closed circles Common Guillemots (n=5 for Whiting to Sprat switch, n=6 for Sprat to Whiting switch). Plotted values are means \pm 1 s.e.m.. Control values are shown for comparison, using the same species symbols; they represent values for acclimated birds on the diet which birds were switched onto. Values plotted for day one are those obtained prior to the switch.

*: values differ significantly from the previous day (repeated measures ANOVA with paired t-test, $p < 0.05$). +: values differ significantly from control values (t-tests).





Effect on digestion parameters of eating a mixed diet

When fed a mixed diet of Whiting and Sprat in the same meal, Common Guillemots showed a significant depression in digestive efficiency, relative to values predicted from their performance on the diets when given separately (paired t-test, $t_5 = 2.75$; $p=0.04$). Digestive efficiency was 4.5% (95% C.I. 0.3 - 8.8%) lower than predicted values. Observed digestive efficiency of Lesser Black-backed Gulls did not differ significantly from predicted values when given a mixed diet (paired t-test n.s.) (Table 4.5).

Table 4.5: Observed and predicted digestive efficiency of birds given mixed meals of Whiting and Sprat.

	predicted digestive efficiency ¹ (%)	observed digestive efficiency (%)
Common Guillemot (n=6)	76.90±1.08	72.37±1.94* (6)
Lesser Black-backed Gull (n=6)	78.53±0.57	78.80±1.27 (6)

¹ See methods for details of calculation of predicted digestive efficiency.

Values presented are mean ±1 s.e.m. percent TMEC_N.

* significantly lower than predicted digestive efficiency (paired t-test, $p < 0.05$).

Effect of acclimation to diet on digestion parameters of Common Guillemots

Over the acclimation period there was a significant increase in digestive efficiency of Common Guillemots on the Whiting diet, although not on the Sprat diet (Table 4.6). Prior to acclimation, there were no between diet differences in retention time, however, by the end of the acclimation period, retention times on the two diets had diverged, such that Whiting was retained for significantly longer than Sprat. This suggests that digestive function did adapt to diet during the acclimation period.

Table 4.6: Digestion parameters of Common Guillemots immediately on removal from the wild (pre-acclimated), and following the three week acclimation period.

Diet		retention time ¹	digestive efficiency ²
Sprat	pre-acclimated (n=6)	5.23±0.20	79.29±1.59
	acclimated (n=5)	4.85±0.11	79.78±0.72
Whiting	pre-acclimated (n=6)	5.03±0.20	72.95±0.27
	acclimated (n=6)	5.29±0.16	74.52±0.35*

¹: Values are mean ± 1 s.e.m. 12 hour retention time (hours).

²: Values are mean ± 1 s.e.m. percent TMEC_N.

* acclimated birds significantly higher digestive efficiency than pre-acclimated birds, t-test $p<0.05$.

DISCUSSION

This work rests on the assumption that captivity did not greatly affect digestion in the experimental birds. All the birds in the experiment remained healthy throughout. Although energy expenditure was presumably reduced by captivity, the balance between energy expenditure and energy intake was not affected (Table 4.1). Thus, we are cautiously confident that the digestion parameters we measured were representative of, if not identical to, those of birds in the wild.

Comparison of digestion parameters on the two diets

Digestive efficiency was considerably higher on Sprat than on Whiting in both bird species in this experiment. Higher digestive efficiency on lipid-rich diets has been recorded in other piscivores (Brugger 1993; Brekke and Gabrielsen 1994; Lawson et al. 1997, but see Bennett and Hart 1993).

One would expect retention times of Sprat to be longer than Whiting, because theoretical predictions are that energy dense foods will be processed in the absorptive regions of the gut for longer than energy dilute foods (Sibly 1981; Martinez del Rio and Karasov 1990; Karasov and Cork 1996), assimilation of energy in lipid is thought to be slow relative to other energy sources (Carey et al. 1983; Place 1996), and *in vitro* gastric digestion of Sprat is slower than that of Whiting (Hilton et al. submitted). While Lesser Black-backed Gulls do show a longer retention time of Sprat than of Whiting, the reverse is true for Common Guillemots. It appears that the Common Guillemot adopts a strategy of rapid and relatively inefficient digestion when eating Sprat.

There was a massive difference in the profitability of the two diets, when considered in terms of energy absorbed per unit mass eaten: an average 6.25 kJ and 6.55 kJ of metabolisable energy per of sprat were obtained by Common Guillemot and Lesser Black-backed Gull respectively, compared to 3.19 kJ and 3.25 kJ per gram wet mass of Whiting. Both Sprat and Whiting commonly occur in the diets of seabirds in the North Atlantic (Cramp and Simmons 1977; 1983; Cramp 1985), and similar variation in the energy density of prey species is experienced by other seabird communities (e.g. Steimle and Terranova 1985). There is also seasonal and size-related variation

of similar magnitude within fish species (Wallace and Hulme 1977; Montevecchi and Piatt 1984; Hislop et al. 1991). It seems clear that prey selection by seabirds should be very strongly influenced by energy density, in addition to more obvious attributes of the prey such as abundance, distance from the colony and ease of capture.

Effects of digestive challenges

Predicted changes in gut function due to acclimation

Prior to diet switches, birds were acclimated to one of the diets for three weeks. Previous work suggests that enzyme and nutrient transporter activity (Karasov 1996), microanatomy (Brugger 1991; Starck and Kloss 1995), gross morphology (Miller 1975; Savory and Gentle 1976; Lee and Houston 1995) and retention time (Levey and Karasov 1992; Lodge 1994; Afik and Karasov 1995; Hume and Biebach 1996) can all change considerably within this time scale in response to diet changes, and our results show that there were changes in digestive function of Sprat and Whiting birds over the acclimation period.

There were several differences between the two diets which might have caused differences in gut function to arise between Sprat and Whiting acclimated birds, and which might thereby result in reduced digestive performance when birds were switched between diets, or given mixed diets. Firstly, Whiting-fed birds ate nearly twice as much as Sprat-fed birds during the acclimation period, so we might expect Whiting-acclimated birds to have larger guts than Sprat-acclimated birds (Moss 1972; Karasov 1996). Secondly, because the Sprat was slower to be digested than Whiting in *in vitro* assays, sprat-acclimated birds might have increased gastric motility, muscular power, protease activity, or acidity relative to Whiting acclimated birds, in order to break down the Sprat quickly. Piersma et al. (1993) reported enormous differences in gastric musculature between Red Knots *Calidris canutus* eating shellfish and those eating soft food pellets. Alternatively Sprat-acclimated birds might simply show longer gastric retention times than Whiting-acclimated birds (Custer and Pitelka 1975). Third, the much higher lipid content of Sprat might result in differences in digestive enzyme activity, coupled with differences in transporter activity, between birds acclimated to the different diets (Karasov 1996). Stomach pH and bile production have important influences on the digestion of lipid

(Stevens and Hume 1995), and might also be expected to differ between birds acclimated to different diets.

The effect of diet switching will depend on the degree to which specialisation of gut function occurs during the acclimation period, and on the rate of response of the gut to a change in diet. It will also of course also depend on whether the difference between the diets is sufficiently large to make a measurable impact on gut function.

Cost of switching diet

The effects of diet switching on Lesser Black-backed Gulls are consistent with a divergence in gut capacity between Sprat- and Whiting-acclimated birds, such that the guts of the latter, which are adapted to processing large quantities of poor quality food, are larger than those of the former. Thus when switched onto smaller amounts of an energy dense food, the large guts of the Whiting-acclimated birds can achieve higher digestive efficiency for the same retention time. Likewise, the smaller guts of the Sprat-acclimated birds can only maintain digestive efficiency on larger amounts of Whiting if they increase retention time above control values. Supra-normal digestive function in birds switched from poor to good diets was not apparent in diet switch experiments of Savory and Gentle (1976) or Lodge (1994). We assume that acclimated birds have optimal gut size and digestive function for their diet, and that, therefore, the Whiting-acclimated birds are not genuinely better adapted to eating Sprat than Sprat-acclimated birds. Presumably the extra energetic cost of maintaining the larger gut (see Schmidt-Nielsen 1990) exceeds the energy advantage gained from having higher digestive efficiency, so that the cost of the diet switch is incurred at the whole animal level, rather than being directly measurable in digestion parameters.

For Whiting-acclimated Common Guillemots, there was a clear and major cost associated with switching to Sprat. Birds showed a dramatic reduction in both retention time and digestive efficiency, which appeared to represent a physiological malfunction. This was despite the fact that Sprat-acclimated Common Guillemots had normal digestion parameters on the Sprat diet. This type of reaction to a switch onto a very nutrient rich diet is known to veterinary scientists (Arnall and Keymer

1975); it was also observed in Harp Seals (*Phoca groenlandica*) during the first week on a very lipid-rich diet of Herring (Lawson *et al.* 1997).

Both Lodge (1994) and Afik and Karasov (1995) reported reduced digestive efficiency in birds following diet switches, although Savory and Gentle (1976) did not, even though their switched birds had markedly different gut morphology to control birds.

Cost of eating a mixed diet

To our knowledge it has not previously been shown that mixing more than one food type in a single meal reduces overall digestive efficiency, though it is not perhaps entirely surprising. If enzyme activity, stomach pH and gastric motility are all rapidly modulated in response to characteristics of the diet, it cannot be possible to optimise these parameters simultaneously for more than one food type. This observation of a measurable reduction in digestive efficiency in a species eating two similar types of fish in the same meal suggests that where diets are more radically different, this effect could be large.

Digestion strategies of Common Guillemots and Lesser Black-backed Gulls

Common Guillemots, as predicted, suffered a greater cost than Lesser Black-backed Gulls when subjected to digestive challenges: Common Guillemots showed a strong adverse reaction when switched to Sprat, and a reduced digestive efficiency when challenged with a mixed diet. The gulls improved their digestive efficiency on both diets over the days immediately following a diet switch, whereas Common Guillemots did not.

In addition Common Guillemots appear to have more rapid and inefficient digestion under normal conditions. The question then arises - what does the Common Guillemot gain in return for paying the cost of this apparently inflexible and inefficient digestion strategy? We suggest that the Common Guillemot might gain by having a high rate of energy assimilation (as a result of rapid digestion), and accepts the cost of having less efficient digestion and a reduced capacity for rapid digestive modulation. There are a number of reasons why Common Guillemots might benefit from such a strategy: they have high metabolic rates relative to gulls (Bennett and Harvey 1987; Bryant and Furness 1995), and therefore a high rate of

energy assimilation might be particularly important. They may also benefit to a relatively large extent from the mass saving that rapid digestion brings about (Sibly 1981). Because of their extremely high wing loading, Common Guillemot flight energy costs are extremely high (Pennycuick 1987; 1989); they frequently also have long foraging ranges (Bradstreet and Brown 1985). By modelling daily energy expenditure of gulls and Common Guillemots, we have shown that rapid but inefficient digestion can produce large energy and time savings for Common Guillemots, but less so for gulls (Hilton *et al.* submitted).

An association between diet, digestive strategy and feeding ecology has been suggested for birds of prey (Barton and Houston 1993a; 1993b; 1994). The present study supports this idea of a co-evolved suite of traits: Common Guillemots are dietary specialists, and appear to have relatively fast and inefficient digestion, which permits rapid energy assimilation, but is relatively poor at responding to digestive challenges. Lesser Black-backed Gulls by contrast are dietary generalists, with slower and more efficient digestion, which responds better to digestive challenges. Related conclusions were drawn by Lee and Houston (1993), who found that the stenophagous Field Vole (*Microtus agrestis*) was markedly less able to adapt its gut morphology in response to dietary challenges than the euryphagous Bank Vole (*Clethrionomys glareolus*).

Decisions involved in diet switching and diet mixing

In common with other studies (Levey and Karasov 1989; Lodge 1994; Afik and Karasov 1995), this study provides evidence that the decision to switch and mix diets is not simply contingent on changes in prey availability and profitability, but must also involve potential digestive consequences. When diet switching occurs, there is in some circumstances a cost to pay, both immediately in terms of reduced digestive performance, and subsequently in the costs of modifying gut structure and function in response to the new diet.

Thus animals are faced with a dilemma: an animal that chooses to specialise on one particular food type benefits by acclimating to that diet. Its digestive function will, over a period of time, become optimal for its diet. However, the more strongly acclimated to one particular diet an animal becomes, the greater the adjustment that

must be made if a diet switch becomes necessary. Thus Common Guillemots taken from the wild at Hornøy, where they had apparently been eating a mixture of a lipid rich and lipid poor fish, were able to digest the Sprat diet in a normal way. However some of the Common Guillemots which had been fed an unvarying diet of Whiting for three weeks and were then switched to Sprat suffered major disruption to digestive function. An animal can, instead of specialising, eat a mixture of food items, and thereby avoid paying the potential future cost of having to make a sudden switch. However, if it does this there may be a continuous present price to pay, because digestive performance is non-optimal when a mixture of foods are eaten together.

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LITERATURE CITED

- Afik D, Karasov WH (1995) The trade-offs between digestion rate and efficiency in warblers and their ecological implications. *Ecology* 76: 2247-2257
- Arnall L, Keymer IF (1975) Bird diseases: an introduction to the study of birds in health and disease. T.F.H. Publications, London
- Barton NWH, Houston DC (1993a) A comparison of digestive efficiency in birds of prey. *Ibis* 135: 363-371
- Barton NWH, Houston DC (1993b) The influence of gut morphology on digestion time in raptors. *Comp Biochem Physiol A* 105: 571-578
- Barton NWH, Houston DC (1994) Morphological adaptation of the digestive tract in relation to feeding ecology of raptors. *J Zool (Lond)* 232: 133-150
- Bennett DC, Hart LE (1993) Metabolizable energy of fish when fed to captive Great Blue Herons (*Ardea herodias*). *Can J Zool* 71: 1767-1771
- Bennett PM, Harvey PH (1987) Active and resting metabolism in birds: allometry, phylogeny and ecology. *J Zool (Lond)* 213: 327-363
- Blaxter KL, Graham NM, Wainman FW (1956) Some observations on the digestibility of food by sheep, and on related problems. *Brit J Nutr* 10: 69-91
- Bradstreet MSW, Brown RGB (1985) Feeding ecology of the Atlantic Alcidae. In: Nettleship DN, Birkhead, TR (ed.s) *The Atlantic Alcidae: The evolution, distribution and biology of the Auks inhabiting the Atlantic Ocean and adjacent water areas*. Academic Press, London, pp 264-318
- Brekke B, Gabrielsen GW (1994) Assimilation efficiency of adult Kittiwakes and Brünnich Guillemots fed Capelin and Arctic Cod. *Polar Biol* 14: 279-284
- Brugger KE (1991) Anatomical adaptation of the gut to diet in Red-winged Blackbirds (*Agelaius phoeniceus*). *Auk* 108: 562-567
- Brugger KE (1993) Digestibility of three fish species by Double-crested Cormorants. *Condor* 95: 25-32
- Bryant DM, Furness RW (1995) Basal metabolic rates of North-Atlantic seabirds. *Ibis* 137: 219-226

- Carey MC, Small DM, Bliss CM (1983) Lipid digestion and absorption. *Ann Rev Physiol* 45: 651-677
- Cramp S (1985) Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic; Volume 4: Terns to Woodpeckers. Oxford University Press, Oxford
- Cramp S, Simmons KEL (1977) Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic; Volume 1: Ostrich to Ducks. Oxford University Press, Oxford
- Cramp S, Simmons KEL (1983) Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic; Volume 3: Waders to Gulls. Oxford University Press, Oxford
- Crisp DJ (1971) Energy flow measurements. In: Holme NA, McIntyre AD (ed.s) *Methods for the study of marine benthos*. Blackwell Scientific Publications, Oxford, pp 197-279
- Custer TW, Pitelka FA (1975) Correction factors for digestion rates for prey taken by Snow Bunting (*Plectrophenax nivalis*). *Condor* 77: 210-212
- Harris LE (1966) Biological energy interrelationships and glossary of energy terms. *Nat Acad Sci Publ* 1411, Washington D.C.
- Hislop JRG, Harris MP, Smith JGM (1991) Variation in the calorific value and total energy content of the Lesser Sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. *J Zool (Lond)* 224: 501-517
- Hume ID, Biebach H (1996) Digestive-tract function in the long-distance migratory Garden Warbler, *Sylvia borin*. *J Comp Physiol B* 166: 388-395
- Hunt GLJ (1972) Influence of food distribution and human disturbance on the reproductive success of Herring Gulls. *Ecology* 53: 1051-1061
- Jackson S, Duffy DC, Jenkins JFG (1987) Gastric digestion in marine vertebrate predators: *in vitro* standards. *Funct Ecol* 1: 287-291
- Karasov WH (1992) Tests of the adaptive modulation hypothesis for dietary control of intestinal nutrient transport. *Am J Physiol* 263: R 496-R 502

- Karasov WH (1996) Digestive plasticity in avian energetics and feeding ecology. In: Carey C (ed) Avian Energetics. Chapman & Hall, New York, pp 61-84
- Karasov WH, Cork SJ (1996) Test of a reactor-based digestion optimization model for nectar-eating Rainbow Lorikeets. *Physiol Zool* 69: 117-138
- Kenward RE, Sibly RM (1977) A Woodpigeon (*Columba palumbus*) feeding preference explained by a digestive bottleneck. *J Appl Ecol* 14: 815-826
- Kersten M, Visser W (1996) The rate of food-processing in the Oystercatcher - food-intake and energy-expenditure constrained by a digestive bottleneck. *Funct Ecol* 10: 440-448
- Lawson JW, Miller EH, Noseworthy E (1997) Variation in assimilation efficiency and digestive efficiency of captive Harp Seals (*Phoca groenlandica*) on different diets. *Can J Zool* 75: 1285-1291
- Lee WB, Houston DC (1993) The effect of diet quality on gut anatomy in british voles (microtinae). *J Comp Physiol B* 163: 337-339
- Lee WB, Houston DC (1995) The rate of change of gut anatomy in voles in relation to diet quality. *J Zool (Lond)* 236: 341-345
- Levey DJ, Karasov WH (1989) Digestive responses of temperate birds switched to fruit or insect diets. *Auk* 106: 675-686
- Levey DJ, Karasov WH (1992) Digestive modulation in a seasonal frugivore, the American Robin (*Turdus migratorius*). *Am J Physiol* 262: G 711-G 718
- Lodge AJ (1994) The effect of diet quality and environmental factors on gut structure and function in the Starling, *Sturnus vulgaris* (L.). PhD thesis, University of Reading
- Martinez del Rio C, Brugger KE, Rios JL, Vergara ME, Witmer M (1995) An experimental and comparative study of dietary modulation of intestinal enzymes in European Starlings (*Sturnus vulgaris*). *Physiol Zool* 68: 490-511
- Martinez del Rio CM, Karasov WH (1990) Digestion strategies in nectar- and fruit-eating birds and the sugar composition of plant rewards. *Am Nat* 136: 618-637
- Miller MJ, Reinecke KJ (1984) Proper expression of metabolizable energy in avian energetics. *Condor* 86: 396-400

- Miller MR (1975) Gut morphology of Mallards in relation to diet quality. *J Wildl Mgmt* 39: 168-173
- Montevecchi WA, Piatt J (1984) Composition and energy contents of mature inshore spawning Capelin (*Mallotus villosus*) - implications for seabird predators. *Comp Biochem Physiol A* 78: 15-20
- Moss R (1972) Effects of captivity on gut lengths in Red Grouse. *J Wildl Mgmt* 36: 99-104
- Pennycuik CJ (1987) Flight of auks (alcidae) and other northern seabirds compared with southern procellariiformes - ornithodolite observations. *J Exp Biol* 128: 335-347
- Pennycuik CJ (1989) Bird flight performance: A practical calculation manual. Oxford University Press, Oxford
- Penry DL, Jumars PA (1987) Modelling animal guts as chemical reactors. *Am Nat* 129: 69-96
- Piersma T, Koolhaas A, Dekinga A (1993) Interactions between stomach structure and diet choice in shorebirds. *Auk* 110: 552-564
- Piersma T, Lindstrom Å (1997) Rapid reversible changes in organ size as a component of adaptive behaviour. *TREE* 12: 134-138
- Place AR (1996) Birds and lipids - living off the fat of the earth. *Poultry And Avian Biology Reviews* 7: 127-141
- Pons J (1994) Feeding strategies of male and female Herring Gulls during the breeding season under various feeding conditions. *Ethol Ecol Evol* 6: 1-12
- Rising JD, Somers KM (1989) The measurement of overall body size in birds. *Auk* 106: 666-674
- Savory CJ, Gentle MJ (1976) Changes in food intake and gut size in Japanese Quail in response to manipulation of dietary fibre content. *Brit Poult Sci* 17: 571-580
- Schmidt-Nielsen K (1990) Animal Physiology: adaptation and environment. Cambridge University Press, Cambridge

- Sibbald IR (1976) A bioassay for true metabolisable energy in feeding stuffs. *Poult Sci* 55: 303-308
- Sibly RM (1981) Strategies of digestion and defaecation. In: Townsend CR, Calow, P (ed.s) *Physiological Ecology: an evolutionary approach to resource use*. Blackwell Scientific Publications, Oxford, pp 109-139
- Starck JM, Kloss E (1995) Structural responses of Japanese Quail intestine to different diets. *Deutsche Tierärztl Wochenschr* 102: 146-150
- Steimle Jr FW, Terranova RJ (1985) Energy equivalents of marine organisms from the continental shelf of the temperate northwest Atlantic. *J Northwest Atl Fish Sci* 6: 117-124
- Stevens CE, Hume ID (1995) *Comparative physiology of the vertebrate digestive system*. Cambridge University Press, Cambridge
- Swennen C, Duiven P (1977) Size of food objects of three fish-eating seabird species: *Uria aalge*, *Alca torda*, and *Fratercula arctica* (Aves, Alcidae). *Neth J Sea Res* 11: 92-98
- Wallace PD, Hulme TJ (1977) The fat/water relationship in the Mackerel *Scomber scombrus* L., Pilchard *Sardina pilchardus* (Walbaum), and Sprat *Sprattus sprattus* (L.), and the seasonal variation in fat content by size and maturity. Ministry of Agriculture, Fisheries and Food, Directorate of Fisheries Research, Lowestoft, England
- Wolynetz MS, Sibbald IR (1984) Relationships between apparent and true metabolizable energy and the effects of a nitrogen correction. *Poult Sci* 63: 1386-1399

chapter 5

WHICH COMPONENTS OF DIET QUALITY AFFECT RETENTION TIME OF DIGESTA IN SEABIRDS?

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Hilton, G.M., D.C. Houston and R.W. Furness. Which components of diet quality affect retention time of digesta in seabirds?

ABSTRACT

The nature of the diet can affect the gut retention time of food consumed by an animal, and a theoretical framework has been developed to explain this in terms of optimal digestion rates. However, diets may differ in a number of different attributes, all of which may separately affect the optimal length of time which they are retained in the gut. Here we attempt to elucidate which of these features are important in determining gut retention time of different fish species when fed to nine north Atlantic seabird species. and discuss the different potential optimisation criteria for retention time in seabirds. Retention times of Lesser Sandeel (*Ammodytes marinus* Raitt.) were shortest, and this species was also rapidly broken down *in vitro*. Sprat (*Sprattus sprattus* (L.)) took longer to be broken down in vitro than Whiting (*Merlangius merlangus* (L.)), and also had a high energy and lipid content, which might be expected to result in slow digestion; yet retention times of the two species were similar. Meal size also had an important effect on gut retention times, large meals being retained for longer in the gut than small meals, apparently due to an upper limit on the peak excretion rate. Diet and meal-size related characteristics are important factors influencing prey profitability, prey selection, and foraging patterns in seabirds.

INTRODUCTION

The rate at which food passes through the gut of animals can have profound effects on whole animal metabolism and energetics. The length of time that food is retained in the gut influences the maximal rate of food ingestion and nutrient assimilation, the efficiency of digestion and absorption of nutrients, and the instantaneous mass of digesta carried (Sibly 1981; Weiner 1992; Barton & Houston 1994; Karasov 1996).

What then determines retention time of digesta? There is ample evidence that characteristics of the food affect retention times. For instance in passerine birds which in the wild consume both fruit and insects, the latter tend to be retained in the gut for longer (Karasov & Levey 1990; Afik & Karasov 1995). A number of diet-associated factors have been examined which apparently affect retention times. These include fibre content, lipid content, particle size, and energy density (see Balch & Campling 1965; Warner 1981; Karasov 1990; Robbins 1993; Stevens & Hume 1995 for reviews). In this paper we consider the factors that might influence retention time of digesta in birds which feed on a diet of fish.

Sibly (1981) modelled the digestive process in animals, and his model gives an illuminating theoretical framework which allows predictions to be made as to how retention time might vary between diets. It is assumed that for any consumer eating any diet there is an optimal retention time which maximises the net rate of energy gain from digestion. This optimal time varies according to the energy gain curve of the diet in question (Figure 5.1).

Before assimilation of energy and nutrient can begin, the food must be physically broken down. In birds, the proventriculus and ventriculus (or gizzard) are the primary sites of food breakdown, through acid proteolysis, and muscular contraction (Stevens & Hume 1995). The strength of the physical and/or chemical defences against digestion will determine the time delay before the subsequent energy gain occurs.

Energy gain begins as nutrient is absorbed in the small intestine. The shape and slope of the energy gain curve describes the rate at which energy gain occurs, and is determined by the kinetics of enzymatic digestion and transport processes (Karasov & Cork 1996). Clearly energy gain through assimilation in the small intestine will

begin before gastric digestion of the meal is complete; thus one can envisage two concurrent energy curves: (1) the (negative) energy curve describing energy expended in gastric digestion; (2) the energy gain curve describing assimilation of energy in the small intestine as a function of time. Sibly's energy gain curve is the sum of these curves. The asymptote of the energy gain curve represents the total amount of available energy in the food.

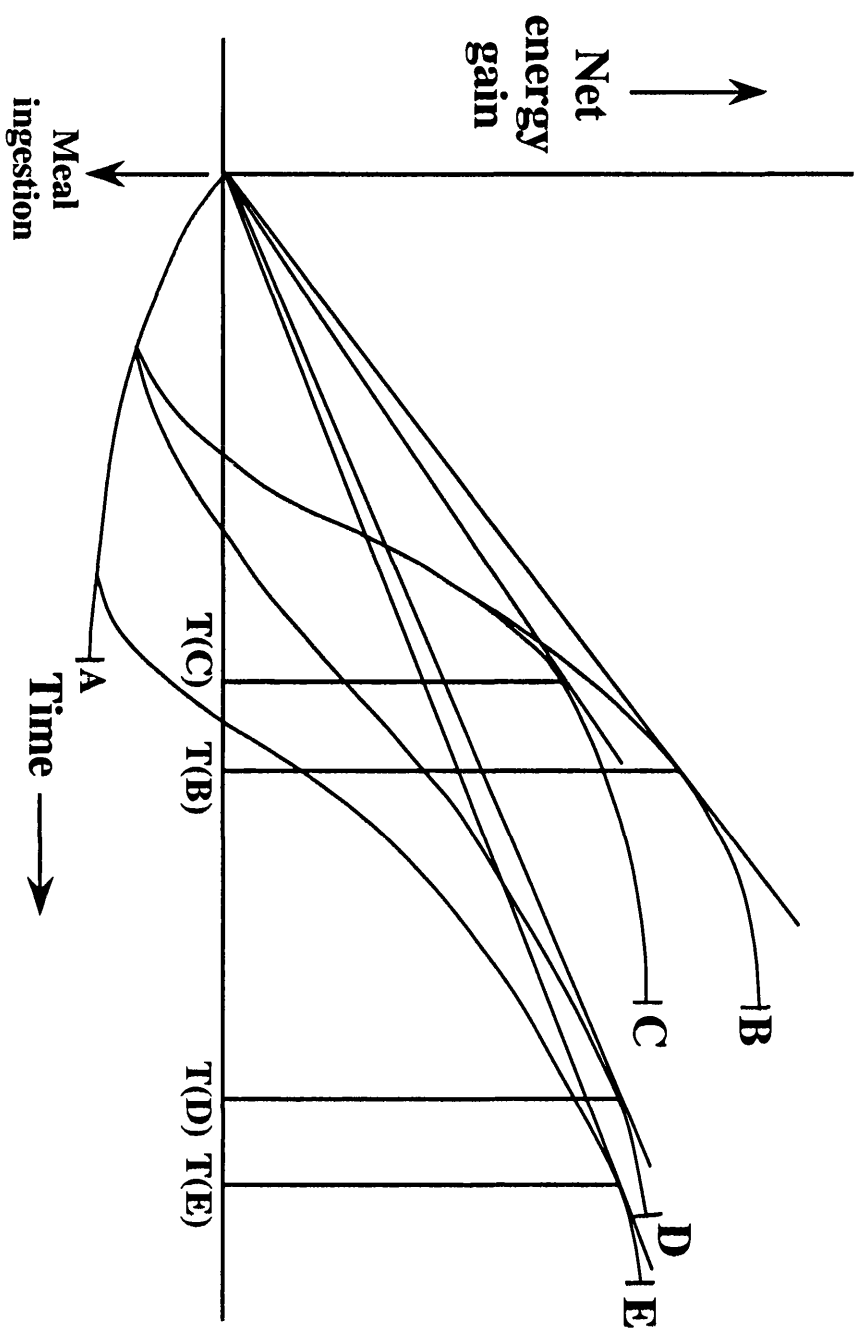
Considering the digestion and assimilation process in this way clarifies the different components that might combine to determine retention times. If we assume that maximising the net rate of energy gain is a major factor influencing retention times, we can predict how retention times may vary between diets: Firstly, if all other characteristics are equal, then retention times should be longer on diets which have strong physical or chemical resistance to breakdown in the stomach. Secondly, retention times should be longer for diets with shallow energy gain curves than for diets with steep energy gain curves, if total energy density and gastric digestion rates are constant. Finally, if rate of energy release, and gastric digestion rates are constant, then retention times will be longer on energy dense diets than on energy dilute diets.

Most studies of between diet variation in retention time have compared diets that are very different in a number of qualitative as well as quantitative ways, e.g. fruit vs. insects (Levey & Karasov 1989; Levey & Karasov 1994; Afik & Karasov 1995). In this paper we report on a study of digesta retention times in nine seabird species eating different types of fish. Fish contains little or no refractory energy (Jackson 1990), and has a nutrient balance similar to that of most consumer tissues. Fermentative chambers are not required, and retention times of digesta are typically short (Wilson *et al.* 1985; Jackson & Ryan 1986; Jackson 1992) (but see Roby, Place & Ricklefs 1985; Roby, Place & Ricklefs 1986; Place & Roby 1986; Roby, Brink & Place 1989; Jackson, Place & Seiderer 1992; Place 1992 for details of digestive adaptations of Procellariiform birds, especially to planktivory). Fish do however vary substantially in energy density, chiefly due to variations in lipid content (Wallace & Hulme 1977; Hislop, Harris & Smith 1991); for this study we selected fish species which varied in lipid content, with the prediction that retention time of digesta in piscivorous birds would vary in response.

We take advantage of an *in vitro* digestibility assay developed by Bigg & Fawcett (1985), and used successfully by Jackson, Duffy & Jenkins (1987) to determine how fish types differ quantitatively in their resistance to gastric digestion. We also determine the energy density and nutrient composition of the fish types using standard chemical methods, to allow us to estimate the asymptote and the relative slope of the energy gain curve. This allows us to relate *in vivo* retention times to all three relevant characteristics of the diet (*in vitro* digestibility, energy density, and nutrient composition). We discuss the results in the light of the predictions made concerning optimal digestion rates.

Fig 5.1: Diagrammatic representation of energy gain by a consumer from different food types (adapted from Sibly 1981).

Curve A: energy loss curve due to gastric digestion of food. Time on curve A represents time taken for gastric breakdown of food. B - E - curves for four different food types.. Slope of gain curve indicates rate of energy gain once breakdown has occurred. Asymptote of gain curve represents total available energy in food. $T(B) - T(E)$ - optimal retention time if gut capacity is limiting (Sibly 1981): Curve B: easily digested, rapidly assimilated, high energy content; Curve C: easily digested, rapidly assimilated, low energy content; Curve D: easily digested, slowly assimilated, low energy content; Curve E: difficult to digest, rapidly assimilated, low energy content.



METHODS

Digestion trials

In 1995 non-breeding adults of Northern Fulmar *Fulmarus glacialis* L., Shag *Phalacrocorax aristotelis* L., Great Skua *Catharacta skua* Brun., Black-legged Kittiwake *Rissa tridactyla* (L.), Herring Gull, *Larus argentatus* Pont., Common Guillemot *Uria aalge* (Pont.), Razorbill *Alca torda* L., and Atlantic Puffin *Fratercula arctica* L. were captured by noose, baited trap, fouling net or cannon net. All species were captured at Foula, Shetland, except Herring Gulls, which were caught in Glasgow. Birds were kept in polythene lined, 60 cm square wire mesh cages. The cages had a 1.5 cm weldmesh floor, suspended 7 cm above the ground on wooden supports. Excreta was collected on plastic trays placed underneath the cages. The trays could be slid in and out of position without unduly disturbing the birds. After capture the birds were fasted until the gut was empty (this was indicated by the production of bile-like faeces). They were then fed at 0800 hours - 0900 hours on the day of the digestion trial. Excreta collections were made at 1, 3, 5, 7, 9 and 12 hours after feeding.

In 1996 juvenile Herring Gulls aged approximately 3 weeks were taken from nests (one per nest) at Walney Island Nature Reserve, Cumbria, and reared in captivity for 3 - 4 weeks, until fledged; during this acclimation period they were fed on the diet which was subsequently used in digestion trials. Gut morphology of birds of this age does not differ significantly from that of adults (G.M. Hilton unpubl. data). In 1997 adult non-breeding Black-legged Kittiwakes, Common Guillemots, Brunnich's Guillemots *Uria lomvia* (L.) and Atlantic Puffins were caught with a noose at breeding colonies on Hornøy, Finnmark, Norway, and digestion trials were performed the following day. In the 1996 and 1997 experiments, birds were kept in 55 cm diameter plastic cages. The trial meal was fed between 0800 and 0900 hours, and excreta collections were as in 1995. All experimental birds were used in only one determination of gut retention time.

Birds in the 1995 experiments were fasted for 12 - 20 hours following capture, prior to the experimental meal, whereas in the 1996 and 1997 experiments the fast was always 12 hours, the birds having been fed on the previous evening. Thus in all

years experimental birds had guts that were empty or very nearly so, although the birds in the 1995 experiment may have had empty guts for a longer period. Lengthy fasts may also affect retention times (e.g. Harlow 1981), probably as a result of metabolic and gut morphology adjustments to a lower plane of nutrition (Klaassen & Biebach 1994; Hume & Biebach 1996). However, in seabird species meals are often taken at infrequent intervals (Furness & Monaghan 1987), and it seems unlikely that fasting related changes to digestion would have occurred in our experimental birds in 1995. To test this we compared retention times of Whiting measured in 1995 (longer fast) and 1997 (shorter fast), for Atlantic Puffin, Common Guillemot and Black-legged Kittiwake. There was no overall effect of trial year on mean retention times (ANOVA model: trial year effect $F_{1,29} = 0.30$, n.s, meal size effect $F_{1,29} = 1.88$, n.s., species effect $F_{2,29} = 3.3$, $p = 0.05$), and no effect of trial year in any of the species treated separately (Mann-Whitney U-tests, trial year 1995 vs. trial year 1997, $p > 0.1$).

Fish diets

Fish of three species were used in the feeding trials: Sprat caught in the southern North Sea during March 1996, and obtained from Lowestoft Fish Supplies, Lowestoft, England; Whiting obtained by research vessels of the Scottish Office Agriculture, Environment and Fisheries Department, Aberdeen, Scotland in the northern North Sea in March 1995 and 1996. and Lesser Sandeel obtained in the Shetland area in May 1995 by Shetland Fish Products, Bressay, Shetland. Fish were stored at -20°C , and thawed immediately prior to feeding. They were moistened and fed at $5 - 10^{\circ}\text{C}$. Birds were fed by hand, except for gulls in 1996, which fed themselves. Frozen storage of fish may have affected their water content and tissue structure, so that digestion of fresh and frozen fish may differ (Jackson *et al.* 1987), but all fish species were stored in the same way.

Determination of mean retention time

Excreta was scraped from the collecting trays using a rubber spatula, and decanted into pre-weighed plastic vials. The collected excreta was frozen at -20°C . Excreta was dried to constant mass at 55°C (120 - 168 hours) in a fan-assisted oven, and dried

samples were weighed to the nearest mg. Mean retention time of digesta was calculated as:

$$t = \frac{\sum_{i=1}^n m_i \cdot t_i}{\sum_{i=1}^n m_i}$$

where m_i is the amount of excreta (g dry mass) produced in the i th time interval, and t_i is the time since the trial meal (Blaxter, Graham & Wainman 1956).

The time period over which mean retention times are calculated affects the absolute values obtained, and it was desirable to test whether it might also affect the comparisons between the diets. In 1995, further excreta collections were made at 19, 21, 23 and 25 hours after the meal. We examined the effect of using 19 and 25 hour mean retention time, instead of 12 hour retention time, on the comparison between Whiting and Sandeel retention times.

To analyse the effect of diet on retention time we used multivariate ANOVA, with wet meal mass as covariate, and species and diet as factors. Since not all seabird species were tested on all diet types, separate analyses were performed for each pair of diets, using only those species for which both of the diets in question had been tested. A full factorial design using unique sums of squares was used, with sequential removal of non-significant interactions, factors and covariates.

Effect of meal size

Meal size may also affect retention times. In general meal sizes differed only slightly between diets, although Whiting meals tended to be somewhat larger than Sprat meals and Lesser Sandeel meals (Table 5.1). Meal sizes were in the range 8.2% - 16.1% of body mass. Average mass of the small Whiting was slightly greater than that of the Sprat (Table 5.1). Sandeel were not measured individually, but were all within 100-125 mm in length, giving a mass of 3.2 - 6.2g, (wet mass = $0.088 \times \text{length (mm)} - 5.49$, $F_{1,14} = 165$, $r^2 = 0.92$, $p < 0.0001$, measurements made on a random sample from the trial batch). Thus individual Lesser Sandeel were much smaller than the other fish types.

In addition to controlling for meal size in the feeding trials, we performed a separate experiment to examine meal size effects on retention time. We measured retention time of six Herring Gulls fed Whiting in a small meal (54.4 ± 2.6 g), an intermediate

meal (104 ± 3.1 g), and a large meal (191.5 ± 4.0 g). Each bird was tested once on each meal size, over three consecutive days. To control for any effect of the order in which meals were presented, each bird was fed the meals in a different order. Experimental procedures were the same as in other experiments in 1996. Repeated measures ANOVA with orthogonal contrasts was used to analyse the effect of meal size on retention time.

***In-Vitro* digestion rates of fish**

Procedures followed those of Jackson *et al.* (1987). Samples of different fish types were standardised by total mass, rather than number of fish. We placed approximately 40 g of whole, freshly thawed fish into plastic mesh bags (9 mm mesh). The samples were warmed in a warm water bath for 15 minutes at 38°C. They were then suspended in 600 ml beakers containing the digestive solution. The solution was composed of 0.6 % Na₂ CO₃, 1% Pepsin (B.D.H. Chemicals Ltd. Pepsin 'A' powder, activity 1 Anson unit per gram), 2% HCl, made up to 400 ml in distilled water. The pH of the solutions was monitored continuously throughout the experiment with a Whatman pH stick, and maintained at 1.15 - 1.30 throughout. If pH approached 1.30, a single drop of HCl was added to the solution. In general pH of the solutions did not change during the experiment; no more than one drop of HCl was added to any sample. Solutions were maintained at 38°C and were gently rotated by hand 10 times per hour. The samples were weighed (± 0.5 g) each hour with a 50 g Pesola balance. The sample was lifted from the solution and rotated gently until no more drops of solution fell off, prior to weighing. Mass of samples was recorded for 14 hours after they were placed in the digestion solutions, by which time digestion was complete in all samples (i.e. no solid material remained in the sample bags) except for some of the Whiting samples, which still held a small amount (<10% of original mass) of material.

We measured *in vitro* digestibility of five fish types: Sprat, Lesser Sandeel, and small and large Whiting from the same batches as were used in feeding trials, and Capelin (*Mallotus villosus* (Müller)) obtained from Icelandic fisheries' surveys. Cumulative digestion curves were plotted for each sample type. We calculated a "mean digestion time" for each sample in the same way as mean retention time was calculated for fish

fed to seabirds (see above). Thus for mean digestion time, m_i was taken as the mass lost by the sample in time interval t_i .

Table 5.1: Mean mass of birds, meals and individual fish used in digestion trials.

	Lesser Sandeel				Sprat		Whiting	
	body mass (g)	meal wet	individual fish	meal wet	individual fish	meal wet	individual fish	meal wet
		mass (g)	wet mass (g)	mass (g)	wet mass (g)	mass (g)	wet mass (g)	mass (g)
Black-legged Kittiwake	366	42.1 ±0.8	3.2 - 6.2	44.7 ±3.3	14.5 ±2.7	44.4 ±4.0	15.2 ±2.0	44.4 ±4.0
Atlantic Puffin	420	42.2 ±2.2	3.2 - 6.2	42.8 ±2.7	13.8 ±2.1	43.7 ±7.1	15.1 ±3.1	43.7 ±7.1
Razorbill	606	68.1 ±2.7	3.2 - 6.2	-	-	78.0 ±6.8	23.6 ±2.3	78.0 ±6.8
Northern Fulmar	686	90.2 ±6.4	3.2 - 6.2	-	-	88.5 ±12.5	22.3 ±3.7	88.5 ±12.5
Herring Gull	907	93.8 ±13.1	3.2 - 6.2	75.5 ±12.0	13.7 ±2.3	104.8 ±11.5	23.1 ±2.7	104.8 ±11.5
Brunnich's Guillemot	926	-	-	75.8 ±0.9	12.2 ±3.9	84.4 ±6.3	21.9 ±3.9	84.4 ±6.3
Common Guillemot	928	102.6 ±2.1	3.2 - 6.2	85.8 ±2.3	12.9 ±2.6	96.8 ±9.3	19.4 ±3.2	96.8 ±9.3
Great Skua	1226	134.8 ±10.5	3.2 - 6.2	-	-	136.9 ±21.6	21.1 ±6.3	136.9 ±21.6
Shag	1451	173.7 ±10.7	3.2 - 6.2	-	-	233.3 ±29.6	25.9 ±4.0	233.3 ±29.6

Chemical composition of fish diets

The aim of measuring the chemical composition of the fish types was to obtain specific values for the nutritional composition of the fish used in the *in vitro* and feeding trial experiments. Our aim was not to compare the relative values of the fish types as prey of wild seabirds, since for most species nutritional composition shows great seasonal and geographic variations (Wallace & Hulme 1977; Hislop *et al.* 1991).

We measured energy, water, nitrogen, lipid and ash content of the four fish species. Each sample consisted of one fish. Samples were thawed, and fresh mass (mg) recorded, before drying to constant mass in a fan-assisted oven at 55°C (96 - 168 hours). A Spex 6700 liquid nitrogen freezer mill was used to homogenise the dried samples, which were subsequently stored in a desiccator. Fractions of the homogenate were then used for determining chemical composition and energy content. Lipid extraction was performed in a Soxhlet apparatus, with boiling chloroform as solvent. Solvent was refluxed 4 - 8 times, until the solvent ran clear. Percent nitrogen content of the samples was determined with a Leco FP-328 Elemental Nitrogen Analyser. Crude protein content was calculated as percent nitrogen x 6.25 (Crisp 1971). Lipid free samples were combusted in a muffle furnace at 650°C for 12 hours in order to obtain ash content. A Parr Adiabatic Bomb Calorimeter with Benzoic Acid standard was used to determine the energy content of dried samples. Chemical composition and energy density are expressed on a wet mass basis. This more accurately reflects the actual value of a fish to a foraging predator than values expressed on a dry mass basis. Sizes of fish in samples were chosen to encompass the range of sizes used in the feeding experiments. We calculated power regressions of chemical composition variables on wet body mass for all fish species, to determine size relationships of chemical composition (Appendix 1).

Statistical analysis was performed using SPSS Version 6.0. Means are presented \pm s.e.m.. Kolmogorov-Smirnov Test was used to test for deviations from normality; all statistical tests are two-tailed.

RESULTS

In-vitro Digestion Rates of Fish Species

There were significant differences between fish types in the rate at which they were digested *in vitro* (One-way ANOVA $F_{4,31} = 40.2$; $p < 0.0001$) (Table 5.2). Post-hoc tests (Tukey's HSD) showed that all fish types differed significantly from each other, except that there was no significant difference between digestion rates of large and small Whiting. Capelin and Lesser Sandeel were digested faster than Sprat and Whiting. Mean digestion time of Sprat was slightly greater than Whiting. *In vitro* digestion rates from fastest to slowest were Capelin > Sandeel > Whiting > Sprat.

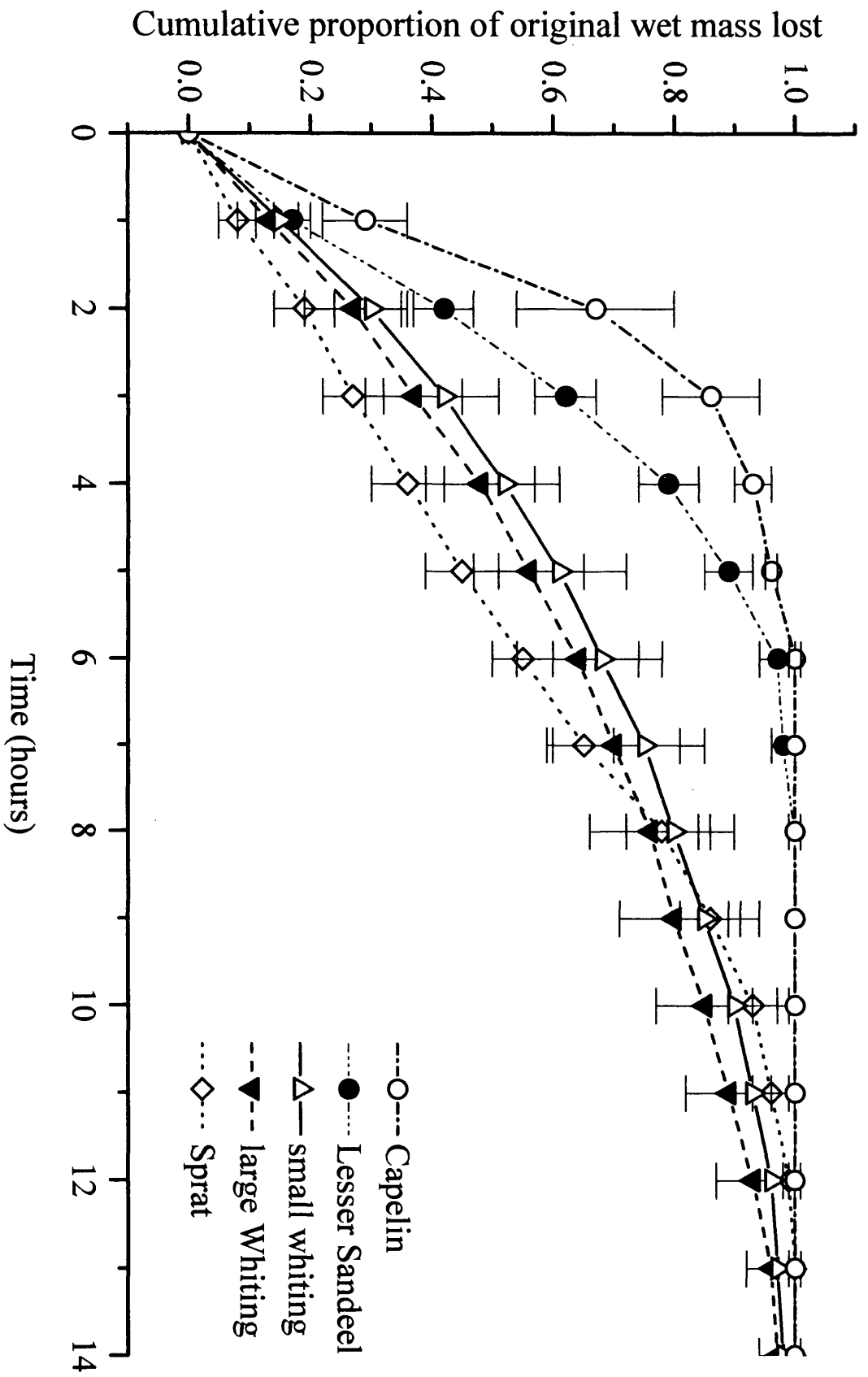
Table 5.2: *In vitro* digestion rates of different fish types.

fish type	mean sample mass (g)	mean fish mass (g)	mean digestion time (hrs)
Capelin	37.3 ±0.30	2.53 ±0.06	2.29 ±0.05
Sprat	38.9 ±0.63	11.63 ±0.15	5.93 ±0.06
Lesser Sandeel	37.3 ±0.30	3.40 ±0.11	3.18 ±0.02
small Whiting	37.0 ±0.05	17.43 ±0.37	4.99 ±0.10
large Whiting	38.9 ±0.69	38.9 ±.69	5.44 ±0.10

n = 8 for all fish types except Capelin (n = 4). Mean digestion time differs significantly between all fish types except small Whiting and large Whiting (Tukey's HSD).

Capelin, Lesser Sandeel and Whiting all showed a negative exponential digestion curve (Figure 5.2). Sprat showed a slightly different trajectory to the other species, being approximately linear for the first eight hours, and then accelerating.

Fig 5.2: *In vitro* digestion rates (\pm s.e.m.) of five different fish types.



Energy density of fish diets

Energy density of Lesser Sandeel ($4.63 \pm 0.05 \text{ kJ g}^{-1}$), and Whiting ($4.40 \pm 0.07 \text{ kJ g}^{-1}$), was relatively low, and did not vary with fish size (Figure 5.3) (expressed on a dry mass basis for comparison with other studies, energy density was $21.5 \pm 0.12 \text{ kJ g dry mass}^{-1}$, and $19.9 \pm 0.20 \text{ kJ g dry mass}^{-1}$ for Lesser Sandeel and Whiting respectively). Sprat tended to have a much higher energy density, which increased with fish size; thus a 5.6 g Sprat (the smallest size used in feeding trials) had a predicted energy density of 5.85 kJ g^{-1} , whereas a 22.6 g Sprat (the largest size used in the feeding trials) had a predicted energy density of 9.47 kJ g^{-1} (corresponding values expressed on a dry mass basis were 23.6 - 28.3 kJ g^{-1}).

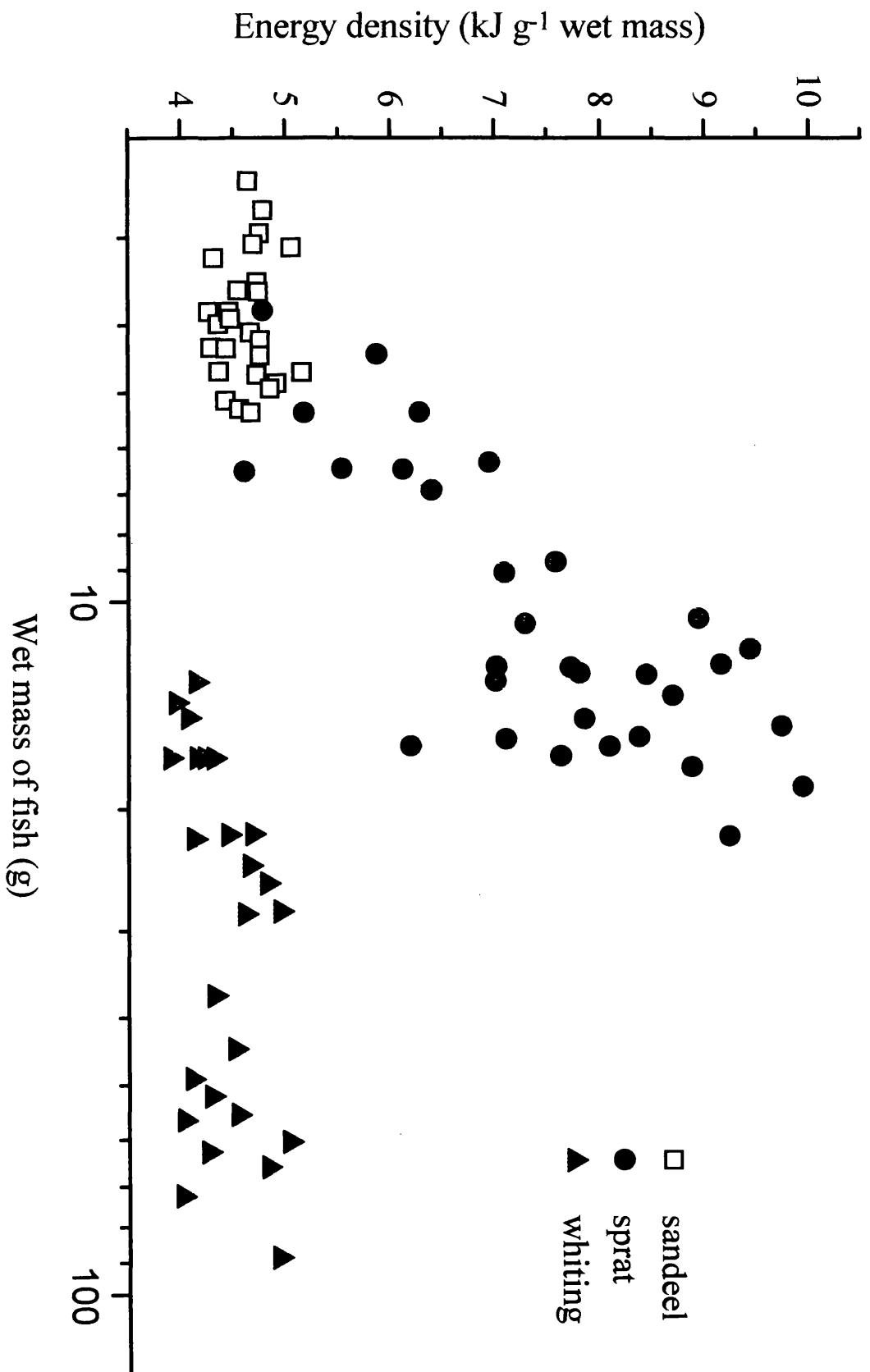
Energy density of Capelin was not measured directly; however their lipid content was similar to Lesser Sandeel and Whiting - slightly higher in the larger Capelin (Table 5.3) - indicating that Capelin energy density lies between 4 - 6 kJ g^{-1} wet mass.

Table 5.3: Proximate chemical composition of fish species used in the experiments.

mean percentage of wet mass								
	water	n	lipid	n	crude protein	n	ash	n
Capelin	78.52 - 73.77	16	1.67 - 4.73	16	-		-	
Lesser Sandeel	78.52 ±0.12	27	2.46 ±0.25	26	15.9 ±0.13	26	3.49 ±0.06	15
Sprat	74.96 - 66.81	47	5.42 - 17.36	16	16	12	3.85 ± 0.11	16
Whiting	77.49 ±0.18	50	2.02 ±0.15	38	15.5 - 16.6	25	3.01 - 4.23	38

Ranges of values are shown where there is a significant relationship between the parameter of interest and fish wet mass. The range describes the predicted values for smallest and largest fish fed to birds.

Fig 5.3: Energy density of Lesser Sandeel, Sprat and Whiting as a function of body mass.



Proximate composition of fish diets

Regressions relating chemical constituents of fish to wet mass are presented in appendix 1. Lipid content was very closely related to energy density (see above). Sprat had a much higher lipid content than the other three species (Table 5.3). Sandeel and Whiting had a low and rather unvarying lipid content, while Capelin had an intermediate lipid content that was size-dependent. There was an extremely close negative relationship between lipid and water content in all species. Thus water content was lower in Sprat than in the other three species. Nitrogen and ash content were rather similar in the three species for which we have data. In Whiting there was a positive relationship between fish size and ash content, such that larger Whiting had higher ash content than Sprat and Lesser Sandeel (Table 5.3).

Effect of meal size on retention times in Herring Gulls

The effect of meal size on retention time of large Whiting meals by Herring Gulls is shown in Figure 5.4. Repeated measures analysis of variance was used to test for a meal size effect. Mauchly's sphericity test indicated no significant heteroscedasticity in the variance-covariance matrix ($W = 0.41$, n.s.). There was a significant effect of meal size on retention time ($F_{2,10} = 8.9$, $p = 0.006$), and orthogonal contrasts indicated that there was no significant difference in retention time between small and moderate meal sizes ($F = 5.9$, n.s), but that retention times were significantly longer on large meals than on small and moderate meal sizes ($F = 30.9$, $p = 0.003$). Peak excretion rate did not vary greatly between meals of different sizes (Fig 5.5a). However, the period of high excretion rate was much more prolonged for large meals than for medium and small meals. The pattern of excretion of medium and small meals was very similar (Fig 5.5).

We therefore have evidence that meal size has an influence on retention times, and hence meal size was included as a covariate in the analysis of the main digestion trials. It should however be stressed that the previous trial demonstrated an effect only over a meal size range of approximately 5 - 20% of body mass - a considerably greater range than that used in the main digestion trials.

Fig 5.4: Retention time of digesta as a function of meal mass for Herring Gulls fed Whiting.

Lines connect values for individual birds.

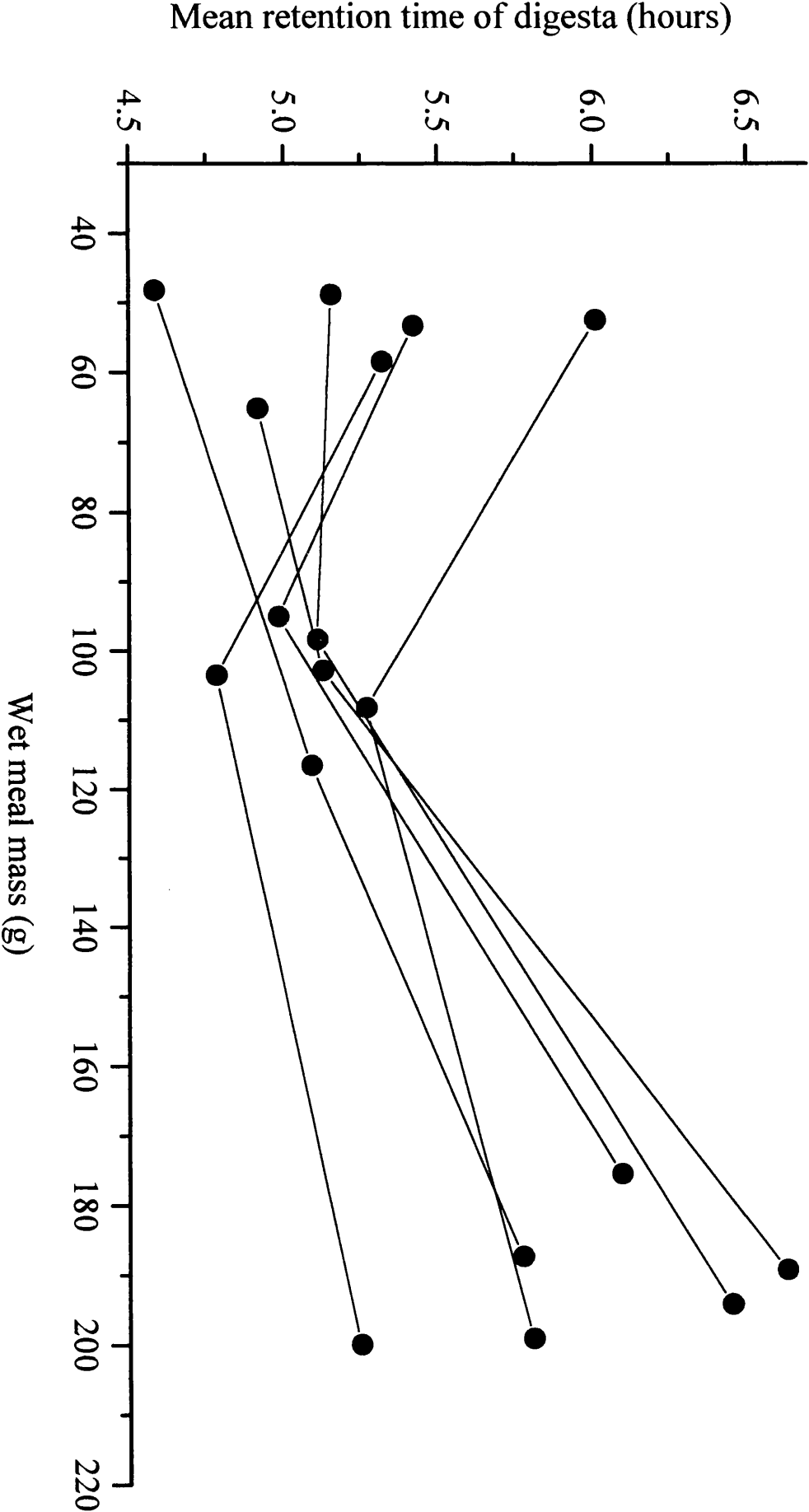
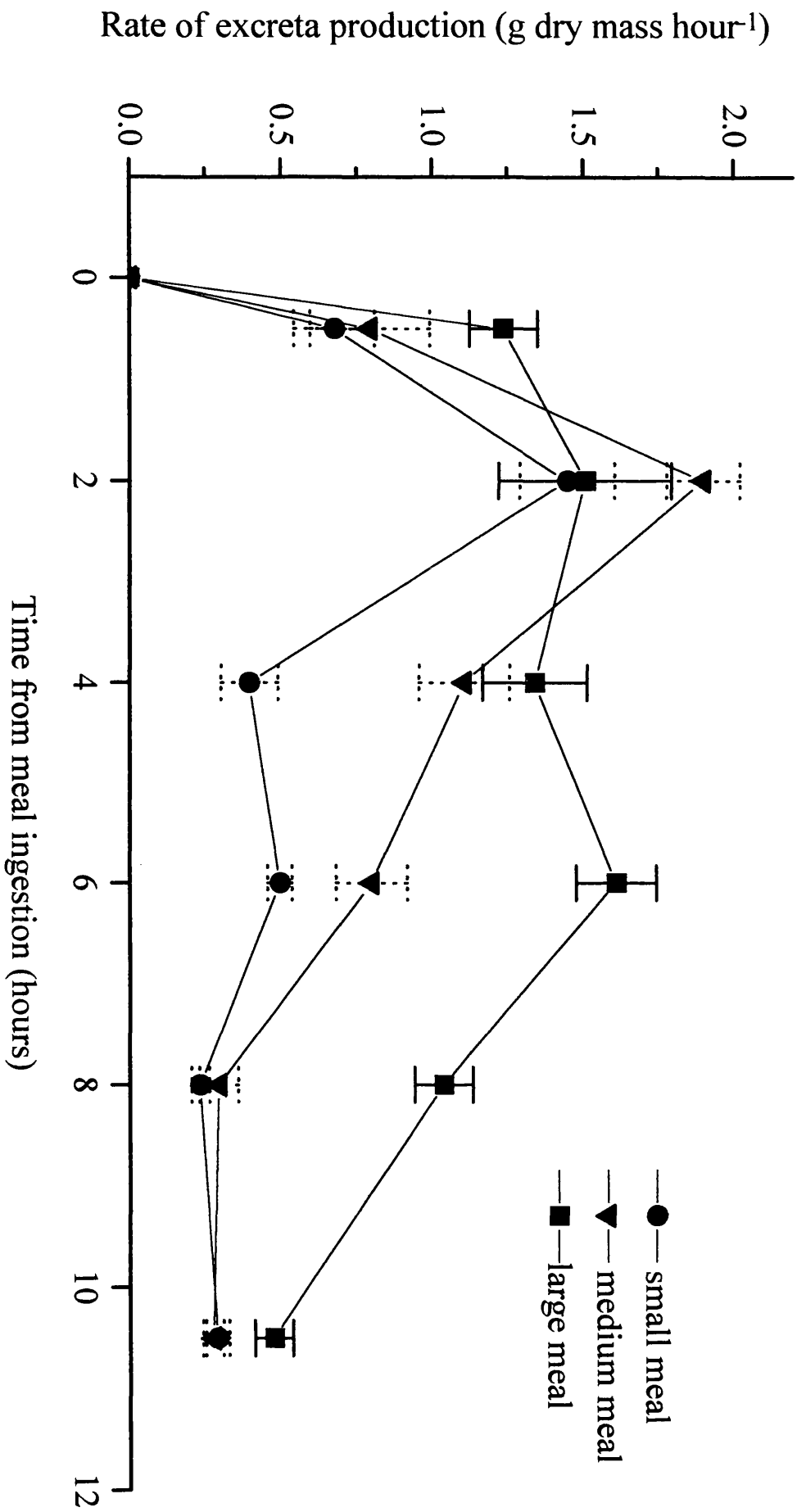


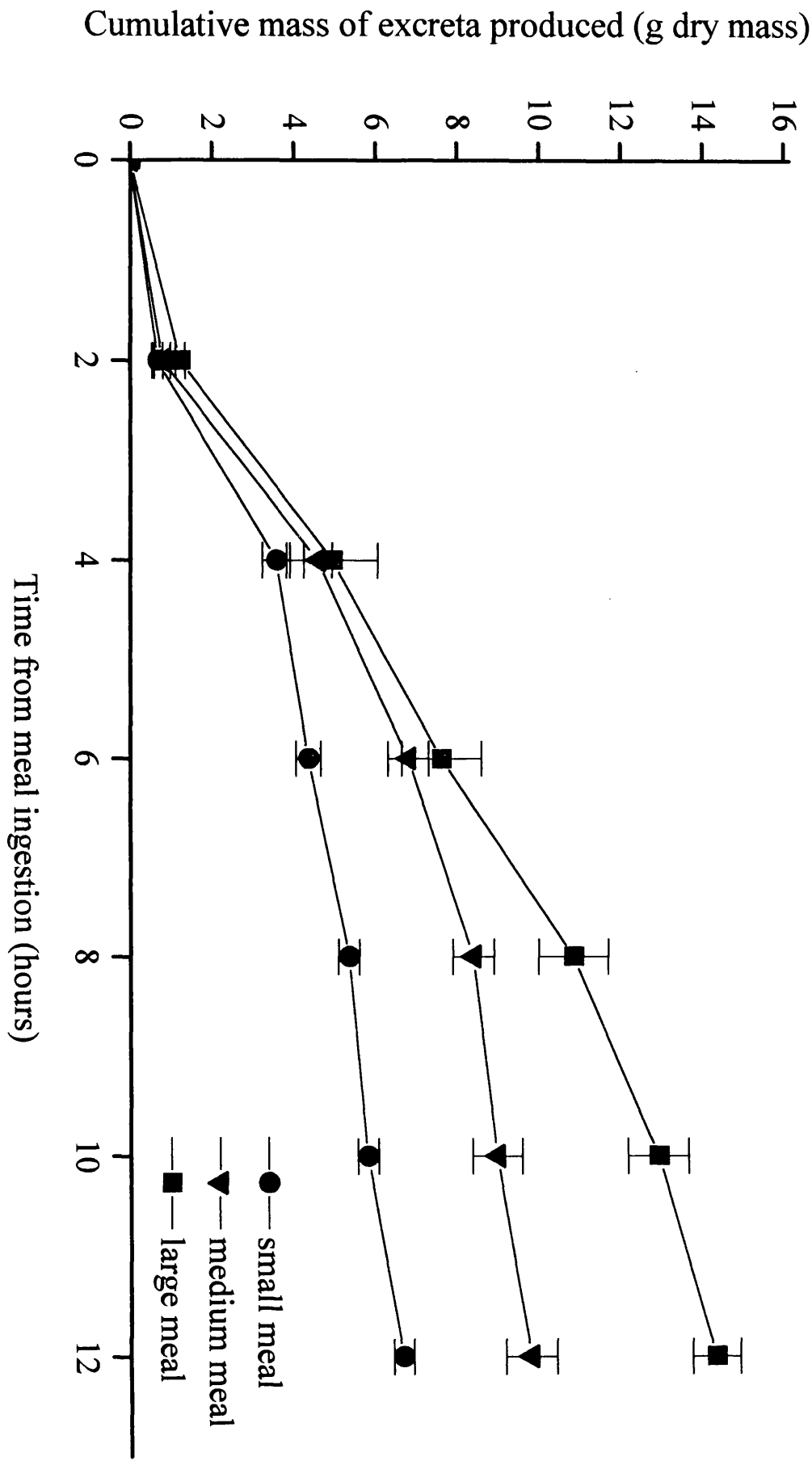
Fig 5.5: Excreta production curves of Herring Gulls fed large, medium and small Whiting meals.

(a) Rate of excreta production (grams dry mass per hour).

Values calculated for each inter-collection interval as total dry excreta mass / number of hours in inter-collection interval.

(b) Cumulative excreta production (g dry mass).





Effect of diet on retention times in seabird species

Table 5.4 shows mean retention times of three diets when fed to nine seabird species. For all seabird species except Northern Fulmar, retention times were shorter when birds were fed Lesser Sandeel than when fed small Whiting (diet effect $F_{1,94} = 9.0$, $p = 0.003$, species effect $F_{8,94} = 21.4$, $p < 0.001$, meal size effect $F_{1,94} = 5.2$, $p = 0.025$, all interaction terms n.s.). For the four seabird species fed Sprat and Lesser Sandeel, retention times were shorter for birds fed the latter fish species than when fed the former (diet effect $F_{1,46} = 16.7$, $p < 0.001$, species effect $F_{4,46} = 4.6$, $p = 0.004$, meal size effect $F_{1,45} = 1.2$, n.s., all interaction terms n.s.). Retention times of Sprat and Whiting were similar for the five seabird species fed on both diets (diet effect $F_{1,72} = 1.8$, n.s., species effect $F_{4,75} = 6.4$, $p < 0.001$, meal size effect $F_{1,73} = 1.1$, n.s., all interaction terms n.s.).

Table 5.4: Mean retention time of fish types fed to seabird species. Retention times were estimated using a gravimetric technique.

species	mean retention time (hours) ¹					
	Lesser Sandeel	n	small Whiting	n	Sprat	n
Black-legged Kittiwake	4.96 ±0.12	5	5.25 ±0.20	11	5.47 ±0.31	6
Atlantic Puffin	4.93 ±0.23	5	5.70 ±0.20	12	6.14 ±0.15	6
Razorbill	4.52 ±0.13	5	5.59 ±0.35	5	-	-
Northern Fulmar	7.30 ±0.31	6	7.12 ±0.18	5	-	-
Herring Gull	5.01 ±0.12	5	5.14 ±0.07	5	5.34 ±0.08	10
Brunnich's Guillemot	-	-	5.04 ±0.35	6	4.87 ±0.21	6
Common Guillemot	4.70 ±0.06	3	5.17 ±0.12	12	4.85 ±0.11	6
Great Skua	5.62 ±0.10	5	5.87 ±0.14	5	-	-
Shag	4.51 ±0.13	5	5.41 ±0.36	5	-	-

¹ All Lesser Sandeel values obtained in 1995. Whiting values obtained in 1995, except: five Common Guillemots, six Black-legged Kittiwakes and five Atlantic Puffins, for which values were obtained in

Mean 12 hour, 19 hour and 25 hour retention times were very highly correlated for species measured in the 1995 experiments, on both Lesser Sandeel and Whiting diets (log-transformed variables, $r \geq 0.92$, $p \leq 0.01$, $n=8$). 19 hour retention time of Lesser Sandeel was significantly shorter than Whiting (diet effect $F_{1,73} = 22.5$, $p < 0.001$, species effect $F_{7,73} = 23.2$, $p < 0.001$, meal size effect $F_{1,72} = 0.22$, n.s., all interaction terms n.s.); and the same applied if 25 hour retention times were used (diet effect $F_{1,74} = 13.7$, $p < 0.001$, species effect $F_{7,74} = 19.6$, $p < 0.001$, meal size effect $F_{1,72} = 0.58$, n.s., all interaction terms n.s.). Thus the time period over which mean retention time was calculated did not appear to affect the ranking of retention times in the bird species, or among the diets. This was because, by 12 hours after the meal, excretion was complete in some Black-legged Kittiwakes, Herring Gulls and Razorbills and was nearly complete in all other species except Northern Fulmar. Incorporating the "tail" of the excretion curve into the calculation of mean retention time seems to have little effect on the relative values obtained.

DISCUSSION

Effect of meal size on retention time

We have demonstrated that meal size can have an effect on gut retention times in Herring Gulls. Retention time of small and medium sized meals was similar, but mean retention time of large meals was greater. Figure 5.6 shows why this occurs: when fed large meals, birds achieved the same peak excretion rate as birds fed medium sized meals, at the same time after the meal, but the high rate of excretion persisted for longer, simply because there was more material to process. By contrast, peak excretion rates were lower for small meals. This is consistent with reactor-theory models of digestion, which predict that the rate of output of material from gut compartments will be proportional to the contents of the compartment (Penry & Jumars 1987). The similar peak excretion rate observed for large and medium meals may represent a maximal rate of food processing, constrained by the physiological limits of the gut. Alternatively it may simply be disadvantageous to process food at a greater rate, because digestive efficiency would be reduced. The implication of these patterns of excretion is that maximal rates of food processing and energy assimilation are likely to be achieved if the gut is kept "topped up", with regular small meals. However, in the breeding season most seabirds alternate rather long nest attendances with foraging trips to discrete, often distant, feeding sites (Furness & Monaghan 1987), and therefore this option is not open to them.

Effect of diet characteristics on retention time

There was good consistency among the seabird species in the ranking of retention times on the different diets. Given this consistency, we are able to rank the *in vivo* retention times of the diets as Lesser Sandeel < small Whiting = Sprat. How does this ranking compare to predictions from theory about optimal digestion rates?

We envisaged three dietary characteristics that might separately influence retention times: *in vitro* digestibility, energy density, and nutrient composition. Table 5.5 summarises the characteristics of the diets that we examined.

In vitro digestibility indicates the rate at which food is broken down in the stomach, and thus the time-lag until energy assimilation can begin (curve A in Fig 1). Among the lipid-poor fish types, *in vitro* digestion rate was negatively correlated with the

size of the individual fish used (Capelin < Lesser Sandeel < small Whiting < large Whiting). This is presumably in part a consequence of a greater surface area : volume ratio in small fish. In general, seabirds are expected to select relatively large individuals of a fish species, because they tend to have higher energy density, and because fewer individuals must be caught for a given meal mass (Harris & Hislop 1978; Hislop *et al.* 1991). The *in vitro* digestibility assay suggests a counter advantage to selection of smaller fish: gastric breakdown will be more rapid. This might increase the maximum rate at which fish can be ingested. Rapid food processing, and hence rapid excretion of digesta, may also be a means of minimising body mass, which confers many advantages on birds (Sibly 1981).

Table 5.5: Summary of the characteristics of the trial diets.

diet	energy composition ¹			
	resistance to digestion	energy density	lipid contribution	protein contribution
Lesser Sandeel	low	low	21%	79%
Sprat	high	high	36 - 65%	64 - 35%
large Whiting ²	moderate	low	14%	86%
small Whiting ³	moderate	low	17%	83%
Capelin	low	low	mainly protein	

¹ protein energy content = 2.36 kJ g⁻¹; lipid energy content = 3.95 kJ g⁻¹ (Robbins 1993)

² energy composition calculated for 50 g fish

³ energy composition calculated for 20 g fish

Energy density and nutrient composition influence optimal retention time by determining the shape of the energy gain curve (curves B - E in Fig 1), after gastric digestion has occurred. Energy density determines the asymptotic energy gain from

a diet; on this basis, optimal retention time of Sprat, which has relatively high energy density, would be longer than that of Lesser Sandeel and Whiting. Nutrient composition determines the slope of the energy gain curve. Assimilation of lipid is thought to be slower than carbohydrate and protein, because emulsification and hydrolysis of fat is a complex process (Carey, Small & Bliss 1983). Therefore one might expect energy gain curves to be more shallow where lipid is the predominant source of energy. Thus on the basis of nutrient composition one would predict relatively long retention times for Sprat, which has a high lipid content compared to the other two diets.

Thus one would predict that, as observed, *in vivo* retention times of Lesser Sandeel would be shortest, because of its high gastric breakdown rate, coupled to low energy density and lipid content. One would also expect that retention times of Sprat would be greater than Whiting, because Sprat is less quickly broken down in the stomach, has higher asymptotic energy gain, and a shallower energy gain curve. However there is no evidence that retention times of Sprat are longer than those of Whiting (Table 5.4). Why might this be so?

The most plausible reason is that the *in vitro* digestion technique fails accurately to mimic gastric digestion, and thereby under-estimates digestion rates of Sprat, relative to Whiting. Although the samples were agitated, they were not squeezed as would happen in a seabird's stomach, due to muscular contractions (Duke 1989; Duke, Place & Jones 1989; Stevens & Hume 1995). Personal observation suggests that Sprat is the more physically fragile of the two species. Thus, although the breakdown through acid proteolysis of the Sprat is slower than Whiting, physical disruption may be more rapid with Sprat. Jackson *et al.* (1987) found that the ranking of *in vitro* digestion rates of seabird prey items - fish > squid > crustacea - was matched by the ranking of *in vivo* gastric digestion rates in seven seabird species (Wilson *et al* 1985; Jackson & Ryan 1986; Jackson 1992).

Secondly, the precise shape of the energy gain curves for the relevant sources of energy - lipid and protein - are not known. Such curves have been determined by means of *in vitro* tissue preparations, for various mono- and disaccharides and amino acids (Karasov & Diamond 1983a; Karasov & Diamond 1983b; Karasov & Diamond

1988; Karasov & Cork 1994; Karasov *et al.* 1986; Martinez del Rio 1990; Martinez del Rio & Karasov 1990;; Martinez del Rio *et al.* 1995). It has not however, to our knowledge, been attempted for complex carbohydrates, proteins or lipids. However, there is ample physiological evidence to support the suggestion that lipid is processed slowly in the avian gut (e.g. Roby *et al.* 1989; Jackson & Place 1990; Place 1992; Place & Stiles 1992), and at the whole animal level, transit time of digesta in Leghorns (*Gallus gallus* (L.)) increased as the level of a lipid supplement was increased from 0% to 30% of the diet (Mateos & Sell 1981; Mateos, Sell & Eastwood 1982).

Is the optimality criterion correct?

We have assumed that the optimal retention time of seabirds is that which maximises the slope of the energy gain curve. However, this strategy is optimal only if further food can be ingested at any time, and in quantities limited by gut capacity (Sibly 1981). For seabirds in the breeding season, meals are discrete and infrequent relative to retention time (Furness & Monaghan 1987), and thus these conditions are frequently not met. The seabird may have a near empty gut for much of the time. In this instance, it may be advantageous to retain digesta in the gut for longer than the slope-maximising time. Thus optimal retention time of seabirds may be closer to Sibly's (1981) first prediction, that energy gain rate will be maximised by retaining food for as long as net energy gain is positive, if gut capacity is not limiting.

Retaining digesta for longer than the slope-maximising time may also be a means of reducing foraging time and energy expenditure (Karasov 1996). It results in increased digestive efficiency (Sibly 1981), and thus less food must be gathered in order to assimilate a given amount of energy. The cost is a reduced maximum energy assimilation rate. Such a digestion strategy has been shown to occur in some nectarivorous birds (Karasov & Cork 1996; Downs 1997), and might be expected in species such as seabirds which are long-lived and slow-breeding, favouring residual reproductive value over current reproductive effort (*sensu* Williams 1966) (Furness & Monaghan 1987). Thus there is reason to think that seabirds may not follow a pure slope-maximising digestion strategy, but instead retain food for somewhat

longer than the slope-maximising time; the extent to which this occurs in different species will be related to their typical meal frequency.

Conclusions

All of the fish types used in these experiments are commonly eaten by north Atlantic seabirds. There were however marked differences between the diets in their *in vitro* digestibility, energy density, and nutrient composition, and this is reflected in variation in their *in vivo* retention times. Two points are clear: firstly, that variation in the digestive characteristics of available fish types can have an important effect on their profitability, in addition to the more obvious characteristics of abundance and ease of capture. Digestive characteristics may thus strongly influence prey selection by seabirds. Differences in the digestive characteristics of food types has been incorporated into models of foraging patterns in herbivores (e.g. Owen-Smith & Novellie 1982; Verlinden & Wiley 1989; Hirakawa 1997), but has yet to be fully recognised as an important factor in the feeding ecology of carnivorous and piscivorous animals. Secondly, there is a need to differentiate between the different components of diet quality. "Diet quality" refers to several separately operating factors, and our understanding of the interplay between digestive function and diet is improved if these factors are made explicit.

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APPENDIX: RELATIONSHIPS BETWEEN FISH COMPOSITION AND WET MASS

Sprat

lipid* = $0.013 \times \text{wet mass}^{1.829}$; s.e. slope = 0.43; $F_{1,14} = 18.5$; $r^2 = 0.54$.

ash = $0.024 \times \text{wet mass}^{1.195}$; s.e. slope = 0.12; $F_{1,14} = 96.6$; $r^2 = 0.86$.

water** = $0.863 \times \text{wet mass}^{0.918}$; s.e. slope = 0.01; $F_{1,29} = 4028$; $r^2 = 0.99$.

nitrogen = $0.048 \times \text{wet mass}^{0.756}$; s.e. slope = 0.24; $F_{1,10} = 10.4$; $r^2 = 0.46$.

Whiting

lipid = $0.029 \times \text{wet mass}^{0.860}$; s.e. slope = 0.18; $F_{1,36} = 22.8$; $r^2 = 0.37$.

ash** = $0.020 \times \text{wet mass}^{1.176}$; s.e. slope = 0.05; $F_{1,23} = 620$; $r^2 = 0.96$.

water = $0.763 \times \text{wet mass}^{1.005}$; s.e. slope = 0.00; $F_{1,48} = 47917$; $r^2 = 1.0$.

nitrogen** = $0.023 \times \text{wet mass}^{1.037}$; s.e. slope = 0.01; $F_{1,36} = 6691$; $r^2 = 1.0$.

Sandeel

lipid = $0.044 \times \text{wet mass}^{0.731}$; s.e. slope = 0.44; $F_{1,12} = 2.8$; $r^2 = 0.12$.

ash = $0.031 \times \text{wet mass}^{1.100}$; s.e. slope = 0.09; $F_{1,13} = 159$; $r^2 = 0.92$.

water = $0.788 \times \text{wet mass}^{0.997}$; s.e. slope = 0.01; $F_{1,13} = 18116$; $r^2 = 1.0$.

nitrogen = $0.024 \times \text{wet mass}^{1.031}$; s.e. slope = 0.04; $F_{1,12} = 773$; $r^2 = 0.98$.

Each regression describes mass of the component (g), as a function of wet mass of the fish (g).

* slope differs from 1.0 (isometry) $p = 0.07$; ** slope differs significantly from 1.0, $p < 0.01$

LITERATURE CITED

- Afik, D. & Karasov, W.H. (1995) The trade-offs between digestion rate and efficiency in warblers and their ecological implications. *Ecology* **76**, 2247-2257.
- Balch, C.C. & Campling, R.C. (1965) Rate of passage of digesta through the ruminant digestive tract. *Physiology of Digestion in the Ruminant* (eds R.W. Dougherty, R.S. Allen, W. Burroughs, N.L. Jacobson, & A.D. McGillard), pp.108-123. Butterworth & Co. London.
- Barton, N.W.H. & Houston, D.C. (1994) Morphological adaptation of the digestive tract in relation to feeding ecology of raptors. *Journal of Zoology (London)* **232**, 133-150.
- Bigg, M.A., & Fawcett, I. (1985) Two biases in diet determination of northern fur seals (*Callorhinus ursinus*). *Marine mammals and fisheries* (eds J.R. Beddington, R.J.H. Beverton, & D.M. Lavigne), pp. 284-291. George Allen & Unwin Ltd., New York.
- Blaxter, K.L., Graham, N.M. & Wainman, F.W. (1956) Some observations on the digestibility of food by sheep, and on related problems. *British Journal Of Nutrition* **10**, 69-91.
- Carey, M.C., Small, D.M. & Bliss, C.M. (1983) Lipid digestion and absorption. *Annual Review Of Physiology* **45**, 651-677.
- Crisp, D.J. (1971) Energy flow measurements. *Methods for the study of marine benthos* (eds N.A. Holme & A.D. McIntyre), pp.197.-279. Blackwell Scientific Publications, Oxford.
- Downs, C.T. (1997) Sugar digestion efficiencies of gurney's sugarbirds, malachite sunbirds, and black sunbirds. *Physiological Zoology* **70**, 93-99.
- Duke, G.E. (1989) Gastrointestinal motility and its regulation. *Poultry Science* **61**, 1245-1256.
- Duke, G.E., Place, A.R. & Jones, B. (1989) Gastric emptying and gastrointestinal motility in Leach's Storm Petrel chicks (*Oceanodroma leucorhoa*). *Auk* **106**, 80-85.
- Furness, R.W. & Monaghan, P. (1987) *Seabird Ecology*. Blackie, Edinburgh.

- Harlow, H.J. (1981) Effect of fasting on rate of food passage and assimilation efficiency in Badgers. *Journal of Mammalogy* **62**, 173-177.
- Harris, M.P. & Hislop, J.R.G. (1978) The food of young Puffins *Fratercula arctica*. *Journal of Zoology* **185**, 213-236.
- Hirakawa, H. (1997) Digestion-constrained optimal foraging in generalist mammalian herbivores. *Oikos* **78**, 37-47.
- Hislop, J.R.G., Harris, M.P. & Smith, J.G.M. (1991) Variation in the calorific value and total energy content of the lesser sandeel (*Ammodytes-marinus*) and other fish preyed on by seabirds. *Journal Of Zoology* **224**, 501-517.
- Hume, I.D. & Biebach, H. (1996) Digestive-tract function in the long-distance migratory garden warbler, sylvia borin. *Journal Of Comparative Physiology* **166B**, 388-395.
- Jackson, S. (1990) Seabird digestive physiology in relation to foraging ecology. PhD thesis, University of Cape Town, Rondebosch, South Africa.
- Jackson, S. (1992) Do seabird gut sizes and mean retention times reflect adaptation to diet and foraging method. *Physiological Zoology* **65**, 674-697.
- Jackson, S., Duffy, D.C. & Jenkins, J.F.G. (1987) Gastric digestion in marine vertebrate predators: *in vitro* standards. *Functional Ecology* **1**, 287-291.
- Jackson, S. & Place, A.R. (1990) Gastrointestinal transit and lipid assimilation efficiencies in three species of sub-antarctic seabird. *Journal Of Experimental Zoology* **255**, 141-154.
- Jackson, S., Place, A.R. & Seiderer, L.J. (1992) Chitin digestion and assimilation by seabirds. *Auk* **109**, 758-770.
- Jackson, S. & Ryan, P.G. (1986) Differential digestion rates of prey by white-chinned petrels (*Procellaria aequinoctialis*). *Auk* **103**, 617-619.
- Karasov, W.H. (1990) Digestion in birds: chemical and physiological determinants and ecological implications. *Studies in Avian Biology* **13**, 391-415.
- Karasov, W.H. (1996) Digestive plasticity in avian energetics and feeding ecology. *Avian Energetics* (ed C. Carey), Chapman & Hall, New York.

- Karasov, W.H. & Cork, S.J. (1994) Glucose-absorption by a nectarivorous bird - the passive pathway is paramount. *American Journal Of Physiology* **267**, G 18-G 26.
- Karasov, W.H. & Cork, S.J. (1996) Test of a reactor-based digestion optimization model for nectar-eating rainbow lorikeets. *Physiological Zoology* **69**, 117-138.
- Karasov, W.H. & Diamond, J.M. (1983a) Adaptive regulation of sugar and amino-acid-transport by vertebrate intestine. *American Journal Of Physiology* **245**, G443-G462.
- Karasov, W.H. & Diamond, J.M. (1983b) A simple method for measuring intestinal solute uptake invitro. *Journal Of Comparative Physiology* **152**, 105-116.
- Karasov, W.H. & Diamond, J.M. (1988) Interplay between physiology and ecology in digestion. *BioScience* **38**, 602-611.
- Karasov, W.H. & Levey, D.J. (1990) Digestive system trade-offs and adaptations of frugivorous passerine birds. *Physiological Zoology* **63**, 1248-1270.
- Karasov, W.H., Phan, D., Diamond, J.M. & Carpenter, F.L. (1986) Food passage and intestinal nutrient absorption in hummingbirds. *Auk* **103**, 453-464.
- Klaassen, M. & Biebach, H. (1994) Energetics of fattening and starvation in the long-distance migratory Garden Warbler *Sylvia borin*, during the migratory phase. *Journal of Comparative Physiology B* **164**, 362-371.
- Levey, D.J. & Karasov, W.H. (1989) Digestive responses of temperate birds switched to fruit or insect diets. *Auk* **106**, 675-686.
- Levey, D.J. & Karasov, W.H. (1994) Gut passage of insects by European Starlings and comparison with other species. *Auk* **111**, 478-481.
- Martinez del Rio, C. (1990) Dietary, phylogenetic, and ecological correlates of intestinal sucrase and maltase activity in birds. *Physiological Zoology* **63**, 987-1011.
- Martinez del Rio, C.M., Brugger, K.E., Rios, J.L., Vergara, M.E. & Witmer, M. (1995) An experimental and comparative-study of dietary modulation of intestinal enzymes in european starlings (*Sturnus vulgaris*). *Physiological Zoology* **68**, 490-511.

- Martinez del Rio, C. & Karasov, W.H. (1990) Digestion strategies in nectar-eating and fruit-eating birds and the sugar composition of plant rewards. *American Naturalist* **136**, 618-637.
- Mateos, G.G. & Sell, J.L. (1981) Influence of fat and carbohydrate source on rate of food passage of semipurified diets for laying hens. *Poultry Science* **60**, 2114-2119.
- Mateos, G.G., Sell, J.L. & Eastwood, J.A. (1982) Rate of food passage (transit-time) as influenced by level of supplemental fat. *Poultry Science* **61**, 94-100.
- Owen-Smith, N. & Novellie, P. (1982) What should a clever ungulate eat. *American Naturalist* **119**, 151-178.
- Penry, D.L. & Jumars, P.A. (1987) Modelling animal guts as chemical reactors. *American Naturalist* **129**, 69-96.
- Place, A.R. (1992) Comparative aspects of lipid digestion and absorption - physiological correlates of wax ester digestion. *American Journal Of Physiology* **263**, R 464-R 471.
- Place, A.R. & Roby, D.D. (1986) Assimilation and deposition of dietary fatty alcohols in Leachs Storm Petrel, *Oceanodroma leucorhoa*. *Journal Of Experimental Zoology* **240**, 149-161.
- Place, A.R. & Stiles, E.W. (1992) Living off the wax of the land - bayberries and yellow-rumped warblers. *Auk* **109**, 334-345.
- Robbins, C.T. (1993) *Wildlife feeding and nutrition*. 2nd edn. Academic Press, London.
- Roby, D.D., Brink, K.L. & Place, A.R. (1989) Relative passage rates of lipid and aqueous digesta in the formation of stomach oils. *Auk* **106**, 303-313.
- Roby, D.D., Place, A.R. & Ricklefs, R.E. (1985) Assimilation of dietary wax esters in seabirds. *Federation Proceedings* **44**, 1762
- Roby, D.D., Place, A.R. & Ricklefs, R.E. (1986) Assimilation and deposition of wax esters in planktivorous seabirds. *Journal Of Experimental Zoology* **238**, 29-41.

- Sibly, R.M. (1981) Strategies of digestion and defaecation. *Physiological Ecology: an evolutionary approach to resource use* (eds C.R. Townsend & P. Calow), pp. 109.-139. Blackwell Scientific Publications, Oxford.
- Stevens, C.E., & Hume, I.D. (1995) *Comparative Physiology of the Vertebrate Digestive System*. Cambridge University Press, Cambridge.
- Verlinden, C. & Wiley, R.H. (1989) The constraints of digestive rate - an alternative model of diet selection. *Evolutionary Ecology* **3**, 264-273.
- Wallace, P.D. and Hulme, T.J. (1977) The fat/water relationship in the Mackerel *Scomber scombrus* L., Pilchard *Sardina pilchardus* (Walbaum), and Sprat *Sprattus sprattus* (L.), and the seasonal variation in fat content by size and maturity. Fisheries Research Technical Report no. 35. Ministry of Agriculture, Fisheries and Food, Directorate of Fisheries Research., Lowestoft.
- Warner, A.C.I. (1981) Rate of passage of digesta through the gut of mammals and birds. *Nutrition Abstracts and Reviews Series B* **51**, 789-820.
- Weiner, J. (1992) Physiological limits to sustainable energy budgets in birds and mammals - ecological implications. *Trends In Ecology & Evolution* **7**, 384-388.
- Williams, G.C. (1966) Natural selection, the costs of reproduction, and a refinement of Lack's Principle. *American Naturalist* **100**, 687-690.
- Wilson, R.P., La Cock, G.D., Wilson, M. & Mollagee, F. (1985) Differential digestion of fish and squid in Jackass Penguins *Spheniscus demersus*. *Ornis Scandinavica* **16**, 77-79.

chapter 6

ORGAN SIZE VARIATION AS A COMPONENT OF LOCAL ADAPTATION IN ICELANDIC SEABIRDS

submitted for publication in *Ecology* as:

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ABSTRACT

The size of body organs shows adaptive temporal variation in many animal species. We tested whether variation in the size of body organs is also a component of local adaptation to ecological conditions. The suite of major body organs was measured in six species of Icelandic seabirds, sampled from two areas where birds experience different ecological conditions. Between-area differences in ecological conditions were consistent among the study species, allowing tests of the generality of ecological effects on organ size. All major body organs showed geographical size variation. Specific predictions concerning how organ sizes should vary geographically were made, based on established relationships between the size of organs and the demands that are placed on them. Between-area organ size differences were largely consistent with these predictions: liver and kidney were large where daily energy expenditure was thought to be large; flight muscle and heart were large where foraging range was large; intestines tended to be large where food energy density was low, and stomachs were large where the food was more resistant to digestion. We conclude that adaptive variation in organ size may be an important means by which animals achieve a close fit to their environment.

INTRODUCTION

The size of body organs shows adaptive plasticity in response to changes in the demands that are placed on them (Hammond and Diamond 1997, Piersma and Lindstrom 1997). For instance, guts increase in size when food intake increases (Savory and Gentle 1976, Kenward and Sibly 1977), and flight muscles get smaller during flightless moulting periods in birds (Piersma 1988). It might therefore be expected that adaptive differences in organ sizes would arise between populations of a species living in different localities, and experiencing different ecological conditions. Evidence for such variation is, however, slight. Here we test the hypothesis that variation in organ sizes will be a component of adaptation to local environment, for six Icelandic seabird species whose organ sizes we measured in two different parts of their range.

Experimental work on animals in captivity (e.g. Speakman and McQueenie 1996), coupled to analysis of temporal changes within wild populations (e.g. Piersma et al. 1996), has established a number of relationships between the size of specific body organs and the demands that are placed upon them. We examined how ecological factors affecting wild populations cause variation in the whole suite of major body organs, using differences in the ecological conditions experienced by our study species in the two sampling areas to make predictions concerning how the size of body organs would differ.

The diet of the study species was sampled at sites around the entire coast of Iceland during the incubation period in 1994 and 1995. In five of the study species (Black-legged Kittiwake *Rissa tridactyla* (L.), Common Murre *Uria aalge* (Pont.), Thick-billed Murre *Uria lomvia* (L.), Razorbill *Alca torda* L., and Atlantic Puffin *Fratercula arctica* L.) there was a clear regional dichotomy in diet: birds from the northern coasts tending to consume Capelin *Mallotus villosus* (Müller) and birds from the southern coasts eating mainly Lesser Sandeel *Ammodytes marinus* Raitt. For details of dietary data by region, see Lilliendahl and Solmundsson (1997). For each of the seabird species, we measured organ sizes of a sample of birds from the "Capelin area", and a sample from the "Sandeel area". Predicted differences in organ

sizes between areas were based on between-area differences in diet, foraging range, and climate.

The feeding ecology of a sixth species, the Northern Fulmar *Fulmarus glacialis* L., does not show the same pattern of between-area variation as the other five species. The difference in diet between areas is not pronounced, and crustacea form a fairly large proportion of the diet at both sites. This species also does not make the same simple commuting trips to foraging grounds that the other species do. Instead Northern Fulmars make very prolonged trips, covering wide areas in a search for prey (Warham 1996). Because they use wind-assisted gliding flight, their energy expenditure is strongly influenced by wind speed (Furness and Bryant 1996). Thus predictions concerning organ size variation were not simple for this species, and we treated it separately in the analyses, predicting that it would show different patterns of organ size variation to the remaining five species.

First, we predict that gut, liver and kidney will be large where foraging range is large, and where water temperature is low. High daily energy expenditure (DEE) necessitates large metabolic supply and processing organs, i.e. gut, liver and kidney (Hammond et al. 1994, Koteja 1996, Hammond and Diamond 1997). For breeding seabirds we would predict high DEE when foraging conditions are poor, such as when foraging range is large (Monaghan et al. 1994, Gabrielsen 1996), and when thermoregulatory costs are high. For diving birds (the four auk species), water temperature differences are likely to be the stronger influence on thermoregulatory costs than air temperature variations, since diving metabolic rate appears to be strongly temperature dependent even at moderate water temperatures (Croll and McLaren 1993, Deleeuw 1996), whereas most northern seabirds have lower critical temperatures in air that are below the air temperatures normally experienced during the breeding season (Gabrielsen et al. 1988).

Second, we consider whether gut size is related to food energy density. Gut capacity tends to vary in proportion to food intake (e.g. Savory and Gentle 1976, Kenward and Sibly 1977), which is related to the energy requirements of the consumer (first prediction), but also to the energy density of the diet, which determines how much food must be eaten in order to assimilate a given amount of energy.

Third, we test the prediction that stomachs will be lighter where the diet is more readily digestible (Piersma et al. 1993 and references therein). Stomach capacity may confound this relationship. For the stomach to have a large capacity (second prediction), extra tissue is required to create a larger chamber, thus the stomach may be heavy even if it has relatively poorly developed musculature. Therefore we also use stomach mass per unit internal surface area as a measure of the strength of stomach musculature.

Finally, we examine the relationship between size of flight machinery (heart and flight muscle) and the foraging range of the birds. It has been shown that flight machinery varies in size in response to the intensity of flight activity (Marsh 1984, Bishop 1997, Jehl 1997). In general, seabirds with large foraging ranges tend to spend more time in flight per day (Cairns et al. 1987, Monaghan et al. 1994). In addition the size of the food load (both chick meals and digesta) carried by the bird will affect flight costs (Pennycuick 1989). Birds with large foraging ranges and low trip frequency may tend to fly home with a greater food load; likewise birds feeding on energy dilute food, or with high DEE are likely to carry greater food loads. If differences in size of heart and flight muscle are related specifically to flight effort, then we would not expect other skeletal muscles to show the same pattern of between area variation. Therefore we also determined leg muscle mass, with the prediction that there would be no between-area differences.

METHODS

We made use of birds that had been collected for diet analyses during the incubation period in 1994 (Lilliendahl and Solmundsson 1997). Organ sizes of ten adult individuals of each of the six species from each of the two diet areas were determined. The auks were collected on the feeding grounds, so for these species it was possible to use distance from the collection site to the nearest breeding colony as an estimate of foraging range. For Black-legged Kittiwake and Northern Fulmar, which were collected as they returned to the nest from feeding trips, such estimates were not possible. Figure 6.1 shows the collection locations of the birds used in the study. Sandeel-feeders were collected from a site on the southern coast and a site on the eastern coast, and Capelin-feeders were from three locations around the northern and north-western coasts. The exception to this was the Thick-billed Murre, which is restricted to northern regions. For this species the Sandeel-feeders were collected from the north-western site, and Capelin-feeders from a northern site.

The birds were weighed at the time of collection, and then double wrapped and frozen at -20°C for 12 - 18 months prior to dissection. Stomachs were removed and frozen separately following removal of food items. Birds were thawed at 5 - 12°C for 12 - 18 hours prior to dissection. All morphometric measurements and organ dissections were performed by GMH. Internal and external morphometrics were measured (± 0.1 mm) using dial calipers. From a large number of morphometric measurements, we selected one variable from each body part (leg, head, trunk and wing) for use in a Principal Components Analysis (PCA) to calculate skeletal body size (Rising and Somers 1989). The variables chosen - wing span, tarsometatarsus length, keel length, and headbill length were those which showed the strongest correlations with other measured variables in the same body part. Skeletal size PCA's were calculated separately for each species. A correlation matrix was used, and the first Principal Component Axis, which we used to estimate skeletal body size, captured 51 - 69% of the variance, with all factor loadings positive.

We dissected the small intestine, heart, liver, kidney, a single pectoralis major muscle, a single supracoracoideus muscle, and the entire musculature of one leg.

Sufficient mesentery and fat were carefully removed from the small intestine using a blunt scalpel to allow it to be straightened. The tissue was allowed to relax in avian ringer solution for 15 minutes prior to measurement, and was then placed on a smooth surface, wetted with avian ringer (Hale 1965). It was straightened, but not pulled out under tension, and the length measured ($\pm 1\text{mm}$) from the pyloric junction to the ileo-caecal junction. The intestine was cut along the line of mesenteric attachment, and the width (circumference) measured at five equidistant points. Average intestine width was determined from these measurements; the length and width variables were used to calculate intestine surface area and intestine volume (assuming a cylindrical shape). The stomach (proventriculus and ventriculus) was prepared and measured in the same manner. For analysis we treated the two stomach compartments as a single organ. Dissected organs were dried to constant mass at 55°C in a fan-assisted oven, and weighed ($\pm 0.001\text{g}$).

To determine whether variations in organ size were related to body condition, we determined body condition of study birds in three ways: visual scoring of abdominal and subcutaneous fat (Hope Jones et al. 1982), calculation of residual mass from log-log regression of body mass on skeletal size³, and determination of lipid content of liver tissue. Lipid extraction from dried liver sub-samples was performed in a soxhlet apparatus using chloroform as a solvent. Diameter of largest follicle and testis length were measured in order to indicate the stage of breeding season (Harris 1964).

We tested for between-area and between-sex body size differences in each species using two-way ANOVA, with skeletal body size as the dependent variable, and sex and area as factors. There was a significant area effect on body size in Atlantic Puffins alone ($F_{1,17} = 21.1$, $P < 0.001$), with Capelin-feeders being significantly larger than Sandeel-feeders. In all species males were bigger on average than females, but this difference was significant only in Black-legged Kittiwake ($F_{1,17} = 11.3$, $P = 0.004$) and Northern Fulmar ($F_{1,16} = 5.84$, $P = 0.03$). Examination of plots of organ sizes with body size indicated that there were no detectable between-sex differences in size-corrected organ masses. Furthermore, the sex-ratios of sample groups differed very little between areas. Therefore we pooled samples of males and females for all species.

To determine between-area differences in organ size, we used size-corrected values. For species with no between-area body size differences we calculated residuals from log-log plots of organ mass on skeletal body size³. For Atlantic Puffin we derived the common slope from the two area-specific regression slopes using ANCOVA, and calculated the intercept of the common regression. Residuals were calculated from this common regression line. Most regressions of organ mass on skeletal body size were non-significant. However, sample sizes were rather small, and in almost all cases the regression slope was positive, hence the decision was taken to perform all analyses on size-corrected values of organ size. For intestine length and width we used log skeletal size, and for intestine and stomach surface area we used skeletal size², as opposed to skeletal size³, as the independent variable for size correction.

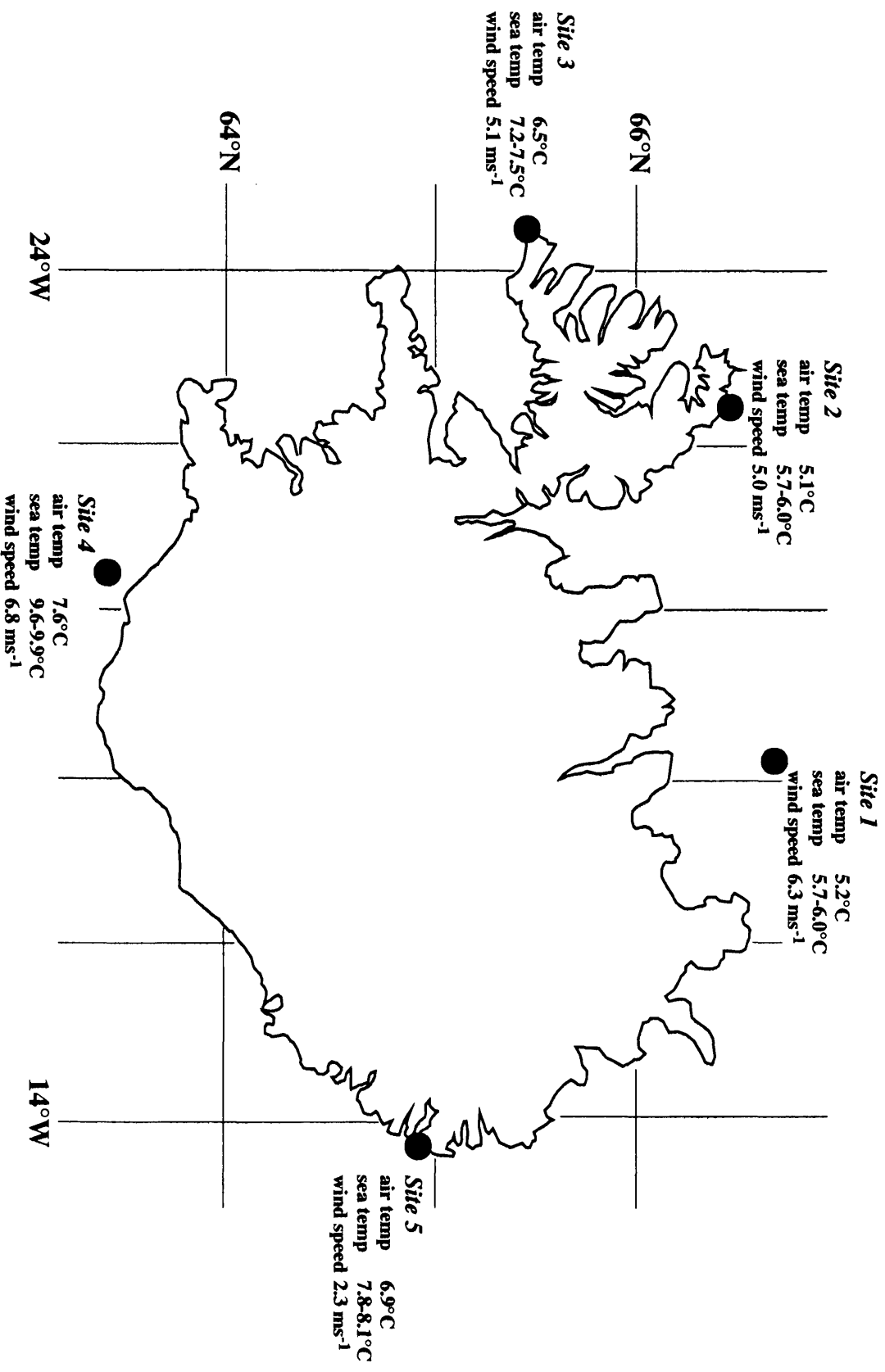
ANOVA models were used to test for the effect of "area" on organ size. The models tested for the significance of an area term ("Capelin area" vs. "Sandeel area"), and a species-area interaction term, using the values for the individuals of the four auk species and Black-legged Kittiwake. There was no species term in the models, because since size-corrected residuals were used, the mean of the values for each species was zero. Our predictions in this study were that heart and flight muscle mass would respond in concert, primarily to the amount of work done in flight, and possibly also diving, whereas liver and kidney mass would covary in response to overall energy expenditure. Thus the area effect for each of these two organ pairs was analysed using a multivariate ANOVA model. In testing for area effects on gut morphology, each variable was analysed separately, as there was no simple *a priori* grouping of gut morphology variables. Where species-area interaction terms were significant, t-tests were used to examine the species - specific effects of area on organ size. The percent differences in organ sizes between areas was estimated by dividing the difference between the back-transformed adjusted mean values for each area by the overall back - transformed mean value. Northern Fulmar data were analysed separately using t-tests. Means are presented \pm s.e.m..

Fig 6.1: Map of Iceland, showing the locations of bird collections, and climate data for the collection sites.

Air temperature and wind speed are means for the month of June 1994 (the month in which collections were made), supplied by the Icelandic meteorological office.

Water temperature data are long term averages for June, supplied by the Levitus 94 website (<http://ingrid.ldgo.columbia.edu/SOURCES/.LEVITUS94/>).

Site 1: Capelin-feeding Common Murre, Razorbill, Atlantic Puffin, Black-legged Kittiwake, Northern Fulmar. Site 2: Capelin-feeding Common Murre, Thick-billed Murre, Northern Fulmar. Site 3: Capelin-feeding Razorbill, Atlantic Puffin, Northern Fulmar. Sandeel-feeding Thick-billed Murre. Site 4: Sandeel-feeding Common Murre, Razorbill, Atlantic Puffin, Black-legged Kittiwake, Northern Fulmar. Site 5: Sandeel-feeding Common Murre, Black-legged Kittiwake.



RESULTS

Diet of seabirds

Energy density of the fish types was taken from literature sources. The larger Capelin eaten by Thick-billed Murre and Black-legged Kittiwake (Table 6.1) are of year class two and above, and have an estimated energy content of 6.4 kJ g^{-1} (Vilhjalmsson 1994). The small Capelin eaten by the remaining species are immature, and have low fat content, with an energy density of around $3.5 - 4.0 \text{ kJ g}^{-1}$ (Montevecchi and Piatt 1984). Lesser Sandeel weighing $6.7 - 14.8 \text{ g}$ have an estimated energy density of 7 kJ g^{-1} during June (Hislop et al. 1991).

Gastric digestion rates of 40 g samples of Lesser Sandeel and Capelin were estimated using an *in vitro* acid-proteolytic digestive solution (G.M. Hilton, D.C. Houston, and R.W. Furness unpublished manuscript). Mean digestion times of Lesser Sandeel (mean mass per fish $3.4 \pm 0.11 \text{ g}$) and Capelin (mean mass per fish $2.5 \pm 0.06 \text{ g}$) were 3.18 ± 0.02 and 2.29 ± 0.05 hours respectively; this difference is highly significant (t-test $t_{10} = 6.50$, $P < 0.001$). The fish used for the *in vitro* digestion rate assay were smaller than those eaten by seabirds in our sample. However, there is no reason to suppose that the ranking of digestibility will change for larger fish, since large Whiting *Merlangius merlangus* (L.) (mean mass per fish $38.9 \pm 0.69 \text{ g}$) were not digested significantly more rapidly *in vitro* than the same overall mass of small Whiting (mean mass per fish $17.4 \pm 0.39 \text{ g}$).

Thus the Capelin-feeders were consuming a diet that was substantially lower in energy density, but easier to break down in the stomach, than the Sandeel-feeders.

Foraging ranges

For all the auk species, apparent foraging range of Capelin-feeders was greater than Sandeel-feeders (Table 6.1). Between-area differences were significant for all species except Razorbill (Mann-Whitney U-tests). In addition, data from research vessel surveys around the coast of Iceland suggest that Capelin shoals tend to occur further offshore than Sandeel shoals (Jonsson 1992; Vilhjalmsson 1994), and that therefore Capelin-feeders have greater foraging ranges than Sandeel-feeders.

Table 6.1: Diet¹, collection dates and foraging ranges² of study birds.

	diet		collection dates (dd.mm)		foraging range (km)	
	north-Capelin	south-Sandeel	north-Capelin	south-Sandeel	north-Capelin	south-Sandeel
Northern Fulmar	67% zooplankton; 33% other fish	75% Sandeel (12.9g); 25% zooplankton	26.06-02.07	31.05		
Black-legged Kittiwake	100% Capelin (6.7g)	100% Sandeel (14.8g)	26.06.94	31.05-19.06		
Common Murre	100% Capelin (4.3g)	100% Sandeel (13.4g)	26.06-02.07	31.05-19.06	59 (15-59)	23 (8-28)
Thick-billed Murre	90% Capelin (8.3g); 10% zooplankton	100% Sandeel (6.1g)	03.07	06.06	86 (86-86)	22 (20-51)
Razorbill	80% Capelin (4.5g); 20% zooplankton	100% Sandeel (6.7g)	08.06-26.06	31.05-01.06	51 (17-57)	21 (18-36)
Atlantic Puffin	44% Capelin (4.5g), 56% zooplankton	100% Sandeel (9.9g)	08.06-26.06	31.05-07.06	17 (17-37)	10 (7-12)

¹ Percentages are the proportion of individuals from that area which contained predominantly that prey species (by mass), discounting birds with empty guts. Values in parentheses are mean calculated fish mass.

² Values are median distance from collection site to nearest breeding colony, with inter-quartile ranges.

Climatic Conditions

Climate data for the different sampling areas are summarised in Figure 6.1. Capelin-feeders experience lower water and air temperatures, and hence greater thermoregulatory costs, than Sandeel-feeders. Wind speeds are slightly greater for northern Fulmars from the Sandeel area than from the Capelin area.

Organ Mass Comparisons

Flight muscle mass and heart mass were significantly greater, by 2% and 7% respectively, in Capelin-feeders than in Sandeel-feeders (Table 6.2). Northern Fulmars also had significantly larger heart and flight muscle masses in the Capelin-areas (student's t-test, $t_{17} = 2.2$, $P = 0.04$ and $t_{17} = 2.12$, $P = 0.05$ respectively). Appendix 1 shows the mean sizes of all measured organs for each species-area combination.

Table 6.2: Results of multivariate ANOVAs of organ mass groups.

	area		species-area interaction		direction of effect
	F ratio	P value	F ratio	P value	
flight muscle/heart	5.64	0.005	1.31	n.s.	Capelin area > Sandeel area
lean liver/kidney	5.58	0.005	2.85	0.005	Capelin area > Sandeel area
leg	0.02	n.s.	1.23	n.s.	-

Degrees of freedom: 2,89 for area and 8,178 for interaction.

No species effect because all values for dependent variable are residuals with mean for each species = 0.

There was also a significant area effect on lean liver and kidney mass, with these organs being heavier in the Capelin-feeding areas (Table 6.2), by 13% and 5.3%

respectively. However, the interaction term was also significant, because the reverse pattern was true in the Thick-billed Murre, though non-significant ($t_{18} = 2.0$, $P = 0.055$ and $t_{18} = 0.50$, n.s. for liver and kidney respectively). Northern Fulmar had larger liver and kidney in the Sandeel-feeding area, but the effect was non-significant in both cases ($t_{17} = 1.70$, n.s. and $t_{17} = 1.34$, n.s. respectively). In contrast to the other body organs, but in agreement with predictions, there were no between area differences in leg mass (Table 6.2).

Sandeel-feeders had 13% greater stomach mass than Capelin-feeders (Table 6.3). By contrast, small intestine mass was 8.1% greater in the Capelin-feeders. In the latter analysis there was a significant species - area interaction, because Sandeel-feeding Common Murre had significantly heavier small intestines than Capelin-feeding Common Murres ($t_{18} = 2.12$, $P = 0.05$). The area effect on stomach mass was non-significant in Northern Fulmar ($t_{16} = 1.44$, n.s.), however, in common with the other four species, Northern Fulmars had significantly heavier small intestines in the Capelin area ($t_{17} = 3.89$, $P = 0.001$).

Table 6.3: Results of ANOVAs of gut morphology variables by area and species.

	area		species-area interaction		direction of effect
	F ratio	P value	F ratio	P value	
stomach mass	30.92	<0.001	1.08	n.s.	Sandeel area > Capelin area
intestine mass	4.97	0.028	4.88	0.001	Capelin area > Sandeel area
intestine length	1.13	n.s.	1.36	n.s.	-
intestine width	0.98	n.s.	3.05	0.021	-

Degrees of freedom for area effects: 1,97 for stomach mass, 1,98 for intestine length, 1,94 for intestine mass, 1,91 for intestine width. df for interaction terms: 4,93 for stomach mass, 4,94 for intestine length, 4,94 for intestine mass and 4,91 for intestine width.

Gut dimension comparisons

Stomach capacity of Sandeel-feeders was 34% greater than that of Capelin-feeders (Table 6.4). The interaction term was significant, even though all species had greater stomach capacity in Sandeel areas, because the magnitude of the effect differed between species. For Northern Fulmars there was no significant area effect on stomach capacity ($t_{15} = 0.88$, n.s.). Intestinal dimensions showed no systematic differences between areas (Table 6.3; Table 6.4). However for Common Murre there was a pronounced area effect, with small intestines being longer ($t_{18} = 2.32$, $P = 0.03$) and wider ($t_{18} = 2.89$, $P = 0.01$) - and hence having greater surface area and volume - in the Capelin-feeding area. For the Northern Fulmar the reverse was true, with intestines being wider ($t_{17} = 3.17$, $P = 0.006$), and having greater surface area and volume, in the Sandeel-feeding area ($t_{17} = 2.18$, $P = 0.04$ and $t_{17} = 2.66$, $P = 0.02$).

Table 6.4. Results of two-way ANOVAs of gut capacity variables by species and area.

	area		species-area		direction of effect
	F ratio	p value	F ratio	p value	
stomach capacity	33.25	<0.001	2.66	0.038	Sandeel area > Capelin area
intestine capacity	1.62	n.s.	3.42	0.01	-
stomach mass : surface area ratio	5.82	0.02	3.44	0.01	Capelin area > Sandeel area
intestine mass : surface area ratio	4.03	0.05	7.78	<0.001	Capelin area > Sandeel area

Degrees of freedom for area effects: 1,92 for stomach capacity and intestine capacity, 1,89 for stomach ratio and 1,88 for intestine ratio. df for interaction terms: 4,92 for stomach capacity and intestine capacity, 4,89 for stomach ratio and 4,88 for intestine ratio.

The lack of a between-area difference in small intestine dimensions, while intestine mass was significantly greater in Capelin areas, was investigated further. We calculated mass per unit area of small intestines (g/cm^2), and performed two-way ANOVA on the log-transformed mass:surface area ratio. There was a significant area effect, with a 9.2% higher mass:surface area ratio in Capelin-feeders (Table 6.4). The interaction term was significant, because for Common Murres the reverse area effect was found ($t_{18} = 4.48$, $P < 0.001$).

A similar examination of stomach mass per unit area was performed (Table 6.4). This indicated that mass:surface area ratio of stomachs was also greater, by 11%, in the Capelin-feeding area. The interaction term was also significant because the reverse trend was apparent, though non-significant, in Black-legged Kittiwake ($t_{16} = 0.39$, n.s.). For Northern Fulmars, stomach mass:surface area ratio was greater in the Capelin-feeding area ($t_{17} = 4.79$, $P < 0.001$).

Body condition and breeding condition

There was no evidence of differences in body condition between areas. Black-legged Kittiwakes in Capelin-feeding areas were significantly heavier for their skeletal size than birds in the Sandeel-feeding areas ($t_{18} = 2.56$, $P = 0.02$), but there was no difference in liver fat or fat scores between areas; for Atlantic Puffin, fat scores were significantly higher in Sandeel-feeders than in Capelin-feeders ($t_{18} = 3.67$, $P = 0.002$), but paradoxically liver fat was higher in Capelin-feeders than in Sandeel-feeders ($t_{18} = 3.027$, $P = 0.007$); Northern Fulmars in Sandeel-feeding areas had higher liver fat than in Capelin-feeding areas ($t_{17} = 3.97$, $P = 0.001$), but not higher fat scores or higher residual mass. It seems safe to infer that body condition differences per se were not a significant influence on organ size variations in this study.

For four of the species there were no significant between-area differences in gonad size, indicating that collections in the two areas were made at similar phases of the breeding season. However, for Common and Thick-billed Murre, gonads tended to be larger in the Sandeel-feeding areas. This is possibly an indication that for these species the collections in the Sandeel-feeding areas were made closer to the egg-laying date than the collections in the Capelin-feeding areas. For Common Murre mean testis length of Capelin- and Sandeel-feeders was 17.9 ± 4.9 mm and $26.3 \pm$

3.2 mm respectively ($t_5 = 2.77$, $P = 0.08$); mean diameter of largest follicle was 4.6 ± 1.1 mm and 10.3 ± 4.1 mm respectively ($t_{10} = 3.27$, $P = 0.02$). For Thick-billed Murre, mean testis length was 11.0 ± 2.1 mm and 27.2 ± 2.8 mm for Capelin- and Sandeel-feeders respectively ($t_7 = 5.43$, $P = 0.001$), while mean follicle diameter was 4.9 ± 0.84 mm, and 29.5 ± 0.85 mm respectively ($t_9 = 6.92$, $P < 0.001$)

DISCUSSION

That organ sizes show temporal variation in animals is now a well established paradigm, which is thought to underpin much of the observed variation in BMR and variation in limits to sustainable metabolic rates (Piersma and Lindstrom 1997). In this study, all of the major body organs show between-area mass differences at the same stage of the breeding season, suggesting that body composition variation may be an important component of adaptation to the local environment, an inference made by Corp et al. (1997) in a study of spatial variation in gut morphology of Wood Mice *Apodemus sylvaticus*.

Most of the organ size variations were in accordance with predictions. The liver and kidney were larger where ecological conditions dictated that DEE would be greater. Increases in liver and kidney size in response to elevated energy demands have been shown in a number of experimental studies (Hammond et al. 1994, Koteja 1996, Speakman and McQueenie 1996). The finding that metabolically active organs were larger in sites where thermoregulatory costs (and other energy costs) are higher, is consistent with the observation that birds living in cold climates tend to have higher resting metabolic rates (Clemens 1988, Root et al. 1991, Klaassen 1995, O'Connor 1996).

Heart and flight muscle were largest where flight activity was predicted to be greater. Leg muscle size showed no between area trend at all, indicating that the effect was due specifically to costs of flight - or possibly in the case of auks costs of diving - rather than to a general trend for bigger skeletal muscle in the Capelin-feeding area. Increases in flight and heart muscle size during the pre-migratory period have been demonstrated in a number of bird species (e.g. Fry et al. 1972, Davidson and Evans 1988, Driedzic et al. 1993), as has flight muscle atrophy during flightless moult periods (Piersma 1988, Gaunt et al. 1990, Jehl 1997). It has also been shown that flight muscle mass can decrease during egg laying (Houston et al. 1995b and references therein), due to mobilisation of stored protein for use in egg production (Kendall et al. 1973, Houston et al. 1995a). The present study shows between-population variation in the size of the flight machinery, outwith these special circumstances.

Gut morphology variations, while very substantial, were more complex. We envisaged two separate influences on stomach morphology: prey toughness, which we predicted would affect stomach mass and mass per unit area; and meal size, which was expected to determine stomach capacity. Sandeel-feeders were expected to have more muscular stomachs that were both heavier, and heavier per unit area, than Capelin feeders, because Sandeels are more resistant to digestion. They would however have smaller stomach capacity, since food intake would be lower for the more energy dense Sandeel. Stomachs of Sandeel-feeders were indeed heavier than Capelin-feeders. However, mass per unit area was actually lower for Sandeel-feeders, while stomach capacity was dramatically greater in the Sandeel-feeders. Piersma et al. (1993) showed that when eating hard shelled molluscs, gizzard muscle thickness of Red Knot *Calidris canutus* is dramatically greater than when eating soft food pellets. Why does the stomach apparently adapt to food toughness in an entirely different way in our study species? Possibly the explanation is that having a large stomach capacity is an adaptation which permits the breakdown of the more resistant Sandeel by improving the mixing ability of the stomach. Increased mass of gastric musculature may be a useful adaptation to crushing prey such as molluscs which have strong external protection, but for breaking down soft-bodied fish it might be more effective to have a vigorous mixing peristaltic action, which would be facilitated by having a large stomach lumen. Jackson et al. (1987) demonstrated that agitation of fish samples greatly increased their rate of breakdown in *in vitro* digestion experiments. Furthermore the oesophagus has a considerably greater capacity than the stomach in the seabird species studied here (G.M. Hilton unpublished data), and therefore the stomach's role in adapting to changes in food intake may be minor.

Small intestines were heavier in the Capelin areas, in accordance with predictions that intestine mass would be greatest where high DEE and low food energy density result in high food intake. Changes in intestinal length and volume (with associated changes in intestine mass) are widespread responses to changes in food intake and energy demands, (e.g. Savory and Gentle 1976, Kenward and Sibly 1977, Ankney and Scott 1988, Hammond and Wunder 1991, Lee and Houston 1993). However, the small intestines of Capelin-feeders in this study had a higher mass, and mass:surface

area ratio, but were not longer or wider, than those of Sandeel-feeders. A greater mass and thickness of intestinal muscle tissue may be an adaptation to more rapid peristaltic flow of digesta, as a result of greater food intake and processing requirements (Brugger 1991). Thickening of the small intestine *laminaria muscularis* following increases in food intake has been recorded in some species (Rubio et al. 1989, Brugger 1991, Starck and Kloss 1995). Common Murres and Northern Fulmars did show between-area differences in intestine dimensions, and furthermore there was a negative relationship between intestine volume and intestine mass. Common Murres have longer and wider intestines in the Capelin areas, but these intestines are lighter and lighter per unit area. Northern Fulmars have heavier intestines in the Capelin area, but intestinal volume is greater in the Sandeel area. It is unclear why these two species show a completely different response to what appears to be the same phenomenon: variation in the volume of digesta that is processed. Changes in gut dimensions which were uncorrelated with intestinal mass changes were noted by Sibly et al. (1990) in Rabbits *Oryctolagus cuniculus* and by Kehoe et al. (1988) in Mallard *Anas platyrhynchos*.

The consistency observed between species in geographical organ size variation suggests that there is a generality of response to ecological conditions; it is particularly relevant that the Northern Fulmar, which was expected to show different patterns of adaptation because it does not fall neatly into the same feeding ecology dichotomy as the other species, did indeed differ markedly in its pattern of organ size variation.

Whether the organ size variation that we have shown is genetic or occurs as a result of reversible phenotypic plasticity is not known. Moss (1972) suggested that changes over several generations in the gut length of captive Red Grouse *Lagopus lagopus scoticus* was due to selection for short-gut genotypes. However, Piersma et al. (1996) demonstrated that the between-race differences in metabolic rate and organ sizes of wild Red Knot disappeared when the two sub-species were kept in similar conditions in captivity. In the present study, phenotypic plasticity seems more likely to be the major factor. Temporal variation in the foraging ecology of these seabirds probably exceeds the spatial variation observed here in the incubation period, and

presumably organ sizes are temporally adjusted in response to these seasonal changes.

For Capelin-feeders, investment in metabolic supply and processing organs, as well as flight machinery, is relatively high. The greater size of metabolically active organs which they sustain in order to meet energy demands may in turn result in high Resting Metabolic Rates (Drent and Daan 1980, Daan et al. 1990, Hammond and Diamond 1997) and high rates of biosynthesis (Cant et al. 1996) - a high input - high output energy strategy. The consequences of this strategy for their life history is of considerable interest.

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APPENDIX: ORGAN MASSES AND GUT DIMENSIONS OF THE STUDY SPECIES, IN THE TWO STUDY AREAS

	Northern Fulmar		Black-legged Kittiwake		Thick-billed Murre		Common Murre		Razorbill		Atlantic Puffin	
	Capelin	Sandeel	Capelin	Sandeel	Capelin	Sandeel	Capelin	Sandeel	Capelin	Sandeel	Capelin	Sandeel
body mass	804 ±81.4	824 ±92.9	448 ±33.1	442 ±23.0	946 ±76.4	941 ±66.3	997 ±58.5	1036 ±41.3	664 ±44	638 ±30.3	565 ±33.9	490 ±42.5
flight muscle	11.6 ±1.81	10.4 ±1.15	10.1 ±0.90	10.3 ±0.95	26.5 ±2.14	25.1 ±1.85	29.2 ±1.73	30.0 ±2.62	16.6 ±1.47	16.0 ±0.52	14.0 ±0.73	12.3 ±0.84
leg muscle	11.4 ±1.92	11.9 ±1.43	2.99 ±0.32	3.08 ±0.21	6.69 ±0.92	6.54 ±0.67	8.37 ±0.75	9.04 ±0.72	5.30 ±0.56	5.05 ±0.39	4.86 ±0.46	4.16 ±0.46
heart	1.85 ±0.30	1.63 ±0.18	1.38 ±0.14	1.30 ±0.10	2.26 ±0.28	1.95 ±0.17	2.25 ±0.25	2.24 ±0.21	1.48 ±0.15	1.45 ±0.14	1.23 ±0.16	1.05 ±0.11
lean liver	5.48 ±0.77	6.23 ±1.50	4.91 ±0.83	4.29 ±0.60	11.1 ±2.10	13.1 ±2.11	12.5 ±1.53	11.7 ±1.42	8.12 ±1.46	6.99 ±1.04	6.84 ±0.93	5.20 ±0.69
kidney	1.64 ±0.28	1.81 ±0.32	1.37 ±0.11	1.27 ±0.15	2.72 ±0.23	2.80 ±0.36	3.17 ±0.29	3.01 ±0.18	2.26 ±0.15	2.21 ±0.23	1.96 ±0.22	1.68 ±0.10
intestine mass	3.03 ±0.48	2.26 ±0.35	1.44 ±0.22	1.61 ±0.65	5.92 ±0.64	5.15 ±0.91	5.34 ±0.88	6.23 ±0.93	2.91 ±0.60	2.60 ±0.69	2.74 ±0.72	1.72 ±0.45

	Northern Fulmar		Black-legged Kittiwake		Thick-billed Murre		Common Murre		Razorbill		Atlantic Puffin	
	Capelin	Sandeel	Capelin	Sandeel	Capelin	Sandeel	Capelin	Sandeel	Capelin	Sandeel	Capelin	Sandeel
intestine length	1409 ±166	1471 ±153	730 ±87.6	714 ±62.7	1369 ±53.3	1368 ±157	1190 ±122	1090 ±58.8	1244 ±130	1266 ±69.4	872 ±70.4	858 ±63.1
intestine width	15.4 ±0.88	17.4 ±1.87	19.4 ±0.84	20.2 ±1.61	24.7 ±2.96	23.5 ±1.98	24.9 ±2.14	22.8 ±1.08	21.1 ±1.69	22.5 ±1.76	21.7 ±1.44	21.2 ±1.73
intestine capacity	26.6 ±4.25	36.3 ±10.6	2.20 ±0.35	2.38 ±0.41	67.0 ±16.2	60.2 ±10.1	59.5 ±12.7	45.0 ±4.20	44.1 ±8.37	51.4 ±898	32.8 ±6.07	31.0 ±7.02
intestine mass:	0.14	0.09	0.10	0.10	0.18	0.16	0.18	0.25	0.11	0.09	0.15	0.09
surface area ratio	±0.02	±0.03	±0.01	±0.03	±0.03	±0.03	±0.03	±0.03	±0.03	±0.03	±0.05	±0.02
stomach mass	4.78 ±0.70	4.37 ±0.67	1.36 ±0.17	1.60 ±0.18	2.49 ±0.35	2.77 ±0.51	2.48 ±0.35	3.00 ±0.21	2.08 ±0.21	2.16 ±0.24	1.42 ±0.20	1.60 ±0.11
stomach capacity	26.8 ±6.69	49.0 ±52	5.20 ±2.19	5.51 ±1.76	15.4 ±5.39	21.9 ±7.67	11.3 ±4.94	17.1 ±9.40	9.97 ±4.60	19.9 ±5.28	2.95 ±0.88	4.69 ±1.00
stomach mass:	0.96	0.89±0.5	0.86	0.93	0.68	0.63	0.90	0.90	0.75	0.48	1.07	0.89
surface area ratio	±0.22	1	±0.21	±0.13	±0.13	±0.18	±0.26	±0.34	±0.20	±0.09	±0.24	±0.16

Values are means ± s.d.. Masses are dry mass of tissue (g), except for body mass, which is fresh mass at death, after subtracting mass of stomach contents. Intestine length and width in mm. Intestine and stomach capacity in ml. Mass:surface area ratios are g cm²

LITERATURE CITED

- Ankney, C.D., and D.M. Scott. 1988. Size of digestive organs in breeding Brown-headed Cowbirds, *Molothrus ater*, relative to diet. *Canadian Journal of Zoology* **66**: 1254-1257.
- Bishop, C.M. 1997. Heart mass and the maximum cardiac output of birds and mammals: implications for estimating the maximum aerobic power input of flying animals. *Philosophical Transactions of the Royal Society of London B* **352**: 447-456.
- Brugger, K.E. 1991. Anatomical adaptation of the gut to diet in Red-winged Blackbirds (*Agelaius phoeniceus*). *Auk* **108**: 562-567.
- Cairns, D. K., K. A. Bredin, and W. A. Montevecchi. 1987. Activity budgets and foraging ranges of breeding Common Murres. *Auk* **104**: 218-224.
- Cant, J. P., B. W. McBride, and W. J. Croom. 1996. The regulation of intestinal metabolism and its impact on whole animal energetics. *Journal of Animal Science* **74**: 2541-2553.
- Clemens, D. T. 1988. Ventilation and oxygen-consumption in Rosy Finches and House Finches at sea-level and high-altitude. *Journal of Comparative Physiology B* **158**: 57-66.
- Corp, N., M. L. Gorman, and J. R. Speakman. 1997. Apparent absorption efficiency and gut morphometry of Wood Mice, *Apodemus sylvaticus*, from two distinct populations with different diets. *Physiological Zoology* **70**: 610-614.
- Croll, D. A., and E. McLaren. 1993. Diving metabolism and thermoregulation in Common and Thick-billed Murres. *Journal of Comparative Physiology B* **163**: 160-166.
- Daan, S., D. Masman, and A. Groenewold. 1990. Avian basal metabolic rates - their association with body-composition and energy-expenditure in nature. *American Journal of Physiology* **259**: R 333-R 340.
- Davidson, N. C. and P. R. Evans. 1988. Prebreeding accumulation of fat and muscle protein by arctic-breeding shorebirds. Pages 342-352 in H. Ouellet, editor. *Acta XIX*

Congressus Internationalis Ornithologici, Ottawa, 22-29 June 1986. University of Ottawa Press, Ottawa, Canada.

Deleeuw, J. J. 1996. Diving costs as a component of daily energy budgets of aquatic birds and mammals - generalizing the inclusion of dive-recovery costs demonstrated in Tufted Ducks. *Canadian Journal of Zoology* **74**: 2131-2142.

Drent, R. H., and S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* **68**: 225-252.

Driedzic, W. R., H. L. Crowe, P. W. Hicklin, and D. H. Sephton. 1993. Adaptations in pectoralis-muscle, heart mass, and energy-metabolism during premigratory fattening in Semipalmated Sandpipers (*Calidris pusilla*). *Canadian Journal of Zoology* **71**: 1602-1608.

Fry, C. H., I. H. Ferguson-Lees, and R. J. Dowsett. 1972. Flight muscle hypertrophy and ecophysiological variation of the Yellow Wagtail *Motacilla flava* races at Lake Chad. *Journal of Zoology (London)* **167**: 293-307.

Furness, R. W., and D. M. Bryant. 1996. Effect of wind on field metabolic rates of breeding Northern Fulmars. *Ecology* **77**: 1181-1188.

Gabrielsen, G. W. 1996. Energy expenditure of breeding Common Murres. Studies of high-latitude seabirds. 4: Trophic relationships and energetics of endotherms in cold ocean systems. Pages 49 - 58 in W. A. Montevecchi, editor. *Canadian Wildlife Series Occasional Paper number 91*, Canadian Wildlife Service, Ottawa, Canada.

Gabrielsen, G. W., F. Mehlum, and H. E. Karlsen. 1988. Thermoregulation in four species of arctic seabirds. *Journal of Comparative Physiology B* **157**: 703-708.

Gaunt, A. S., R. S. Hikida, J. R. Jehl, and L. Fenbert. 1990. Rapid atrophy and hypertrophy of an avian flight-muscle. *Auk* **107**: 649-659.

Hale, P. 1965. *Biological Laboratory Data*. Science Paperbacks and Methuen Publishing Co., Bath, UK

Hammond, K. A., and J. Diamond. 1997. Maximal sustained energy budgets in humans and animals. *Nature* **386**: 457-462.

- Hammond, K. A., and B. A. Wunder. 1991. The role of diet quality and energy need in the nutritional ecology of a small herbivore, *Microtus ochrogaster*. *Physiological Zoology* **64**: 541-567.
- Hammond, K. A., M. Konarzewski, R. M. Torres, and J. Diamond. 1994. Metabolic ceilings under a combination of peak energy demands. *Physiological Zoology* **67**: 1479-1506.
- Harris, M. P. 1964. Aspects of the breeding biology of the gulls *Larus argentatus*, *L. fuscus* and *L. marinus*. *Ibis* **106**: 423- 456.
- Hislop, J. R. G., M. P. Harris, and J. G. M. Smith. 1991. Variation in the calorific value and total energy content of the Lesser Sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. *Journal of Zoology (London)* **224**: 501-517.
- Hope Jones, P., B. F. Blake, T. Anker-Nilssen, and O. W. Rostad. 1982. The examination of birds killed in oilspills and other incidents - a manual of suggested procedure. Nature Conservancy Council, Aberdeen, UK.
- Houston, D. C., D. Donnan, and P. J. Jones. 1995. Use of labelled methionine to investigate the contribution of muscle proteins to egg production in Zebra Finches. *Journal of Comparative Physiology B* **165**: 161-164.
- Houston, D. C., D. Donnan, P. J. Jones, I. Hamilton, and D. Osborne. 1995. Changes in the muscle condition of female Zebra Finches *Poephila guttata* during egg laying and the role of protein storage in bird skeletal muscle. *Ibis* **137**: 322-328.
- Jackson, S., D. C. Duffy, and J. F. G. Jenkins. 1987. Gastric digestion in marine vertebrate predators: *in vitro* standards. *Functional Ecology* **1**: 287-291.
- Jehl, J. R. 1997. Cyclical changes in body composition in the annual cycle and migration of the Eared Grebe *Podiceps nigricollis*. *Journal of Avian Biology* **28**: 132-142.
- Jonsson, G. 1992. Icelandic Fishes, second edition. (in Icelandic). Fjølvi, Reykjavik, Iceland.

- Kehoe, F. P., C. D. Ankney, and R. T. Alisauskas. 1988. Effect of dietary fiber and diet diversity on digestive organs of captive Mallards (*Anas platyrhynchos*). Canadian Journal of Zoology **66**: 1597-1602.
- Kenward, R. E., and R. M. Sibly. 1977. A Woodpigeon (*Columba palumbus*) feeding preference explained by a digestive bottleneck. Journal of Applied Ecology **14**: 815-826.
- Kendall, M. D., P. Ward, and S. Bacchus. 1973. A protein reserve in the pectoralis major muscle of *Quelea quelea*. Ibis **115**: 600-601.
- Klaassen, M. 1995. Molt and basal metabolic costs in males of 2 subspecies of Stonechats - the european *Saxicola torquata rubicula* and the east-african *Saxicola torquata axillaris*. Oecologia **104**: 424-432.
- Koteja, P. 1996. Limits to the energy budget in a rodent, *Peromyscus maniculatus* - does gut capacity set the limit. Physiological Zoology **69**: 994-1020.
- Lee, W. B., and D. C. Houston. 1993. The effect of diet quality on gut anatomy in British voles (microtinae). Journal of Comparative Physiology B **163**: 337-339.
- Lilliendahl, K., and J. Solmundsson. 1997. An estimate of summer food consumption of six seabird species in Iceland. ICES Journal of Marine Science **54**: 624-630.
- Marsh, R. L. 1984. Adaptations of the Gray Catbird *Dumetella carolinensis* to long-distance migration - flight-muscle hypertrophy associated with elevated body-mass. Physiological Zoology **57**: 105-117.
- Monaghan, P., P. Walton, S. Wanless, J. D. Uttley, and M. D. Burns. 1994. Effects of prey abundance on the foraging behavior, diving efficiency and time allocation of breeding Guillemots *Uria aalge*. Ibis **136**: 214-222.
- Montevocchi, W. A. and J. Piatt. 1984. Composition and energy contents of mature inshore spawning Capelin (*Mallotus villosus*) - implications for seabird predators. Comparative Biochemistry and Physiology A **78**: 15-20.
- Moss, R. 1972. Effects of captivity on gut lengths in Red Grouse. Journal of Wildlife Management **36**: 99-104.

- O'Connor, T. P. 1996. Geographic variation in metabolic seasonal acclimatization in House Finches. *Condor* **98**: 371-381.
- Pennycuik, C. J. 1989. Bird flight performance: A practical calculation manual. Oxford University Press, Oxford, UK.
- Piersma, T. 1988. Breast muscle atrophy and constraints on foraging during the flightless period of wing molting Great-crested Grebes. *Ardea* **76**: 96-106.
- Piersma, T., L. Bruinzeel, R. Drent, M. Kersten, J. Vandermeer, and P. Wiersma. 1996. Variability in basal metabolic-rate of a long-distance migrant shorebird (Red Knot, *Calidris canutus*) reflects shifts in organ sizes. *Physiological Zoology* **69**: 191-217.
- Piersma, T., A. Koolhaas, and A. Dekinga. 1993. Interactions between stomach structure and diet choice in shorebirds. *Auk* **110**: 552-564.
- Piersma, T., and A. Lindstrom. 1997. Rapid reversible changes in organ size as a component of adaptive behaviour. *Trends in Ecology and Evolution* **12**: 134-138.
- Rising, J. D., and K. M. Somers. 1989. The measurement of overall body size in birds. *Auk* **106**: 666-674.
- Root, T. L., T. P. O' Connor, and W. R. Dawson. 1991. Standard metabolic level and insulative characteristics of Eastern House Finches, *Carpodacus mexicanus* (Muller). *Physiological Zoology* **64**: 1279-1295.
- Rubio, L. A., A. Brenes, and M. Castano. 1989. Histological alterations to the pancreas and the intestinal-tract produced by raw faba bean (*Vicia faba* l minor) diets in growing chicks. *British Poultry Science* **30**: 101-114.
- Savory, C. J., and M. J. Gentle. 1976. Changes in food intake and gut size in Japanese Quail in response to manipulation of dietary fibre content. *British Poultry Science* **17**: 571-580.
- Sibly, R. M., K. A. Monk, I. K. Johnson, and R. C. Trout. 1990. Seasonal variation in gut morphology of wild Rabbits (*Oryctolagus cuniculus*). *Journal of Zoology (London)* **221**: 605-619.

Speakman, J. R., and J. McQueenie. 1996. Limits to sustained metabolic-rate - the link between food-intake, basal metabolic-rate, and morphology in reproducing mice, *Mus musculus*. *Physiological Zoology* **69**: 746-769.

Starck, J. M., and E. Kloss, 1995. Structural responses of Japanese Quail intestine to different diets. *Deutsche Tierärztliche Wochenschrift* **102**: 146-150.

Vilhjalmsson, H. 1994. The Icelandic Capelin stock. *Rit Fiskideildar* **13**: 1-281.

Warham, J. 1996. The behaviour, population biology and physiology of the petrels. Academic Press, London, UK.

GENERAL DISCUSSION

Each chapter in the thesis is a self-contained whole, and has its own discussion of the main points raised. Here I discuss some of the gaps in the present study, and give some speculative ideas about the direction of future research into the relationships between avian digestion and ecology.

This study has been primarily functional in approach. Digestion rate and digestive efficiency are outcomes, rather than processes. More detailed analysis of the physiological determinants of these parameters (such as gut motility and biochemistry) fall outside the scope of this project. Similarly the study of gut morphology neglected micromorphology, which might be a very important factor in explaining variation in digestive function. The functional approach allows adaptive hypotheses to be tested. However, unsupported by detailed knowledge of the processes involved there is a danger that variation (or the lack of it) which is actually a result of mechanical and biochemical constraints is interpreted as having adaptive significance (Gould & Lewontin 1979).

Information gained from digestion trials on wild seabirds is hard won, and labour intensive. Experiments can in general only be conducted in summer, and the feeding and housing requirements of seabirds are large. Many more hypotheses could be tested, with larger sample sizes, if more amenable laboratory based bird species were used. However, many of the digestive adaptations that have been reported from laboratory studies have not yet been shown to affect foraging decisions of birds in the wild, and this is an issue which needs to be addressed. It is clearly very important to return to the field, armed with laboratory-derived ideas and data, to establish the importance of digestive factors in determining foraging patterns of wild animals. Chapter 6 provides an illustration of this: while all of the relationships between organ sizes and ecological conditions had been demonstrated empirically in the laboratory, there is no published information on whether and to what degree such relationships occur in the field.

At present digestive efficiency and digestion rate must almost always be measured in captive trials (but see Prop & Vulink 1992 for retention time estimations made on free-living wild geese). The problem of stress and captivity induced changes in

metabolism have yet to be resolved, and must always be considered as a potentially confounding factor in digestion trials (see Piersma et al. 1996). In the multi-species comparative study reported in chapter 2, stress may have been a factor, since birds were not acclimated to captivity, but metabolic changes were avoided by conducting the trials immediately following removal from the wild. In the experiments on Common Guillemots and Lesser Black-backed Gulls reported in chapter 4, stress was avoided because the birds were acclimated to captivity by the time that the experiments were conducted, but metabolic changes may have occurred due to reduced energy expenditure in captivity. The development of methods for field measurement of digestion parameters should be a priority. Current techniques may be viable in some circumstances. For instance the gull species studied in the present experiment readily eat bait left at the nest site (*pers obs.*). Transit time of visible markers introduced to bait could be determined through direct observation of birds on the nesting territory. Another major breakthrough would be a method of analysing body composition non-destructively. Tomography and ultrasound techniques provide some prospect of success in the near future (Piersma & Lindstrom 1997), offering the possibility of integrating morphology, energetics and digestion studies.

This study provides further evidence of adaptive variation in digestion parameters at inter-specific, inter-individual and intra-individual levels. If adaptational thinking is applied to the digestion paradigm, it is clear that optimal digestion strategies will vary according to the circumstances in which an animal lives. An important point raised by this study is that digestion strategies can vary within a guild of species with superficially similar feeding ecology. Karasov (1990) recognised that between taxon differences in digestion parameters occur, but data which compare digestive efficiency and digestion rates of different species, on the same diets and under the same conditions, have hitherto been scarce. Furthermore, relatively subtle diet shifts between different fish diets can result in significant changes in digestion parameters. The implication of this is that digestive considerations may be an influence on frequent and small scale changes in foraging behaviour, as well as in major shifts such as large-scale migration (Klaassen & Biebach 1994; Hume & Biebach 1996)

and seasonal fruit - seed - insect diet switches (Levey & Karasov 1989; Afik & Karasov 1995).

Reversible plasticity of digestion parameters and gut morphology has been amply demonstrated, and is discussed by Karasov (1996). The nature and extent of digestive plasticity is of interest in itself. However this plasticity also provides an important opportunity to use inter- and intra-individual variation in digestive strategy as a powerful test of ideas concerning the links between digestion and ecology. Recent studies of inter-individual variation have improved the understanding of the adaptive significance of many behavioural phenomena (Cuthill & Houston 1997). Work on within individual plasticity has already yielded exciting information on digestive responses to elevated metabolic demands (Hammond & Wunder 1991; Koteja 1996; Speakman & McQueenie 1996), to the demands of avian migration (Klaassen & Biebach 1994; Hume & Biebach 1996), and to changes in diet and feeding regime (Afik & Karasov 1995; McWilliams & Karasov 1998).

Given this background, the subject of digestion - ecology relationships promises to be a rewarding research topic for the future. Research to date has only begun to explore the interplay between feeding ecology and digestive function, and much remains to be discovered.

I have shown that adaptation to current diet can result in costs when novel diets are eaten, but the experiments reported here could be developed to answer many more questions. Digestive plasticity means that specialising on one feeding regime (diet type, meal size, meal frequency) results in optimisation of digestive function; the greater the degree of specialisation, the greater the likely cost when diets are changed. Thus there is a continually evolving dilemma between specialising and generalising for an individual, and the benefits of specialising must depend on such variable factors as the likelihood of having to make sudden and major diet switches, or the frequency of more subtle diet switches. It is unclear as yet whether the effects reported in chapter 4, and in other diet switching experiments (Levey & Karasov 1989; Lodge 1994; Afik & Karasov 1995), are of sufficient magnitude to have any significant effect on the behaviour of animals in the wild. To be able to show that

digestive considerations have a bearing on diet switching and mixing decisions in nature would be valuable.

As well as the nature of the diet, the size and timing of meals may have a strong bearing on digestive function, although this has not been studied in any detail (but see McWilliams & Karasov 1998 for an initial attempt to address the problem). Are meal size and frequency affected by digestive considerations as well as behavioural considerations? What is the optimal digestive response to irregular meals, malnutrition and starvation? What are the optimal uses of gut tissue under conditions of food shortage? Gut tissue provides a source of metabolisable energy (e.g. Piersma et al. 1996), but presumably use of gut tissue to meet immediate energy demands reduces an animal's ability to take advantage of a return to favourable feeding conditions, because of reduced gut processing capacity (Hume & Biebach 1996). I have some preliminary data on how gut morphology differs between birds that have died of starvation and those that have died whilst well nourished.

Factors intrinsic to the consumer may also affect optimal digestion strategy, as well as the extrinsic effects of diet and feeding regime. In this case optimal digestion strategy can be seen as “state dependent”. many studies, reviewed by Warner (1981) and Karasov (1990), have shown that digestion parameters may differ between individuals of different age, reproductive status or moult status. An explicit use of state-dependent modelling of optimal digestion might be a productive approach to understanding the adaptive significance of these changes.

The relationships between organ size, digestive capacity and ceilings on energy expenditure are the subject of much recent research (see Hammond & Diamond 1997). Further fieldwork of interest would examine links between digestion parameters and energy expenditure in individual wild birds. Daily energy expenditure appears to be extremely variable between individuals in the wild (e.g. Birt-Friesen et al. 1989); do digestion rates and processing capacities vary in response? Do high quality individuals have low energy expenditure and small guts, or the reverse? The answer probably depends on the ecology of the species in question. For long lived and slow breeding seabirds the most successful individuals might be those that can minimise their energy expenditure while still surviving and

rearing chicks; these individuals might be able to maintain energy balance with a small and cheap gut.

The links between individual diet specialisation and digestion are also of interest. This is particularly relevant to seabirds, as in several taxa, notably skuas and gulls (Furness 1987; Pierotti & Annett 1987), there is a high degree of individual specialisation in diet. Variations in digestion as a result of variations in diet might have important consequences for metabolic rates and diet switching ability, which in turn are important in determining the costs and benefits of specialisation.

It has been shown that the size of nutrient reserves are related to an individual's dominance (Witter & Swaddle 1995) (which determines starvation risk in competitive foraging situations), and perceived predation risk (Witter et al. 1994). In a similar way, the balance between the costs and benefits of rapid digestion might be altered by the state of the individual. Slow and efficient digestion with a large gut might tend to be favoured if an individual anticipates future food shortage; rapid digestion and mass reduction might be favoured where predation risk is high.

Physiological cause and effect in individual quality is little understood, but variations in digestive physiology might be an important factor in explaining why some animals are fitter than others. For instance it has been shown that early nutritional status can be an important determinant of quality later in life (Boag 1987). Possibly a favourable nutritional state early in life allows a high quality digestive system to develop, which has positive feedback effects on future fitness.

In conclusion, the use of such concepts as optimality and trade-offs will continue to instruct studies of adaptive variation in digestive function. Moreover, much behavioural ecology research is now concerned with finding the underlying physiological mechanisms of and constraints on behaviour. I hope that this thesis might give some ideas for further research into these areas.

LITERATURE CITED

- Afik, D. & Karasov, W.H. (1995) The trade-offs between digestion rate and efficiency in warblers and their ecological implications. *Ecology* **76**, 2247-2257.
- Birt-Friesen, V.L., Montevecchi, W.A., Cairns, D.K. & Macko, S.A. (1989) Activity-specific metabolic rates of free-living Northern Gannets and other seabirds. *Ecology* **70**, 357-367.
- Boag, P.T. (1987) Effects of nestling diet on growth and adult size of Zebra Finches (*Poephila guttata*). *Auk* **104**, 155-166.
- Cuthill, I.C. & Houston, A.I. (1997) Managing time and energy. *Behavioural Ecology: an evolutionary approach (4th edition)* (eds J.R. Krebs & N.B. Davies), pp.97-120, Blackwell Science, Oxford, UK.
- Furness, R.W. (1987) *The Skuas*. T & A.D. Poyser, London.
- Gould, S.J. & Lewontin, R.C. (1979) The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society B* **205**, 581-598.
- Hammond, K.A. & Diamond, J. (1997) Maximal sustained energy budgets in humans and animals. *Nature* **386**, 457-462.
- Hammond, K.A. & Wunder, B.A. (1991) The role of diet quality and energy need in the nutritional ecology of a small herbivore, *Microtus ochrogaster*. *Physiological Zoology* **64**, 541-567.
- Hume, I.D. & Biebach, H. (1996) Digestive-tract function in the long-distance migratory Garden Warbler, *Sylvia borin*. *Journal Of Comparative Physiology B* **166**, 388-395.
- Karasov, W.H. (1990) Digestion in birds: chemical and physiological determinants and ecological implications. *Studies in Avian Biology* **13**, 391-415.
- Karasov, W.H. (1996) Digestive plasticity in avian energetics and feeding ecology. *Avian Energetics* (ed C. Carey), pp. 61-84, Chapman & Hall, New York.

- Klaassen, M. & Biebach, H. (1994) Energetics of fattening and starvation in the long-distance migratory Garden Warbler, *Sylvia borin*, during the migratory phase. *Journal of Comparative Physiology B* **164**, 362-371.
- Koteja, P. (1996) Limits to the energy budget in a rodent, *Peromyscus maniculatus* - does gut capacity set the limit? *Physiological Zoology* **69**, 994-1020.
- Levey, D.J. & Karasov, W.H. (1989) Digestive responses of temperate birds switched to fruit or insect diets. *Auk* **106**, 675-686.
- Lodge AJ (1994) The effect of diet quality and environmental factors on gut structure and function in the Starling, *Sturnus vulgaris* (L.). PhD thesis, University of Reading.
- McWilliams, S.R. & Karasov, W.H. (1998) Test of a digestion optimization model: effect of variable-reward feeding schedules on digestive performance of a migratory bird. *Oecologia* **114**, 160-169.
- Pierotti, R. & Annett, G. (1987) Reproductive consequences of dietary specialisation and switching in an ecological generalist. *Foraging Behaviour* (ed A.C. Kamil), pp.417-441, Plenum Publishing Corporation, New York.
- Piersma, T., Bruinzeel, L., Drent, R., Kersten, M., Vandermeer, J. & Wiersma, P. (1996) Variability in basal metabolic-rate of a long-distance migrant shorebird (Red Knot, *Calidris canutus*) reflects shifts in organ sizes. *Physiological Zoology* **69**, 191-217.
- Piersma, T., & Lindstrom, Å. (1997) Rapid reversible changes in organ size as a component of adaptive behaviour. *Trends in Ecology and Evolution* **12**, 134-138.
- Prop, J. & Vulink, T. (1992) Digestion by Barnacle Geese in the annual cycle: the interplay between retention time and food quality. *Functional Ecology* **6**, 180-189.
- Speakman, J.R. & McQueenie, J. (1996) Limits to sustained metabolic-rate - the link between food-intake, basal metabolic-rate, and morphology in reproducing mice, *Mus musculus*. *Physiological Zoology* **69**, 746-769.
- Warner, A.C.I. (1981) Rate of passage of digesta through the gut of mammals and birds. *Nutrition Abstracts and Reviews Series B* **51**, 789-820.

Witter, M.S. & Swaddle, J.P. (1995) Dominance, competition and energy reserves in the European Starling, *Sturnus vulgaris*. *Behavioural Ecology* **6**, 343-348.

Witter, M.S., Cuthill, I.C. & Bonser, R.H.C. (1994) Experimental investigations of mass-dependent predation risk in the European Starling, *Sturnus vulgaris*. *Animal Behaviour* **48**, 201-222.

